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THE RIPE HUMAN GRAAFIAN FOLLICLE, TOGETHER WITH SOME SUGGESTIONS AS TO ITS MODE OF RUPTURE

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For the purposes of this paper the ripe Graafian follicle is defined as one which, from its superficial position, its size, and the thickness of the wall separating it from the ovarian surface, there is reason to believe is fast approaching the time at which rupture may take place. Added to this, must necessarily be considered the condition of the contained ovum. If evidence is forthcoming that the ovum is passing through, or has passed, the maturation stage, such is confirmatory proof that so far as the contents of the follicle are concerned they are ready for discharge. If, as not unfrequently happens, the ovum exhibits indications of degenerative changes, these must be taken into account in any estimate that may be formed regarding the normal appearance of the follicle.

Admitting that coincident with its approach to the surface of the ovary, the Graafian follicle enlarges, what are we to regard as the normal measures of its size? One can readily understand that there may be, and are, considerable variations in the dimensions of a follicle which in other respects fulfils the conditions which are to be regarded as indications of its ripeness.

Size of ripe Graafian Follicle. When reference is made to the various British and foreign text-books, it will be found that there is great disparity in the measures given. The dimensions recorded range from 2 mm. to 20 mm., the average size being about 15 mm. in diameter. In my experience this latter figure is much too high. In the specimens I have examined of follicles exceeding a diameter of 5 mm. I have either failed to find a contained ovum or when it was met with, it proved to be in a degenerated condition.

For these reasons a certain amount of caution is necessary before accepting the figures usually quoted, for mere naked eye inspection of the ovary, on section, may be misleading, since though the follicles exposed may be of considerable size, there is no proof that their contents are normal.

Nagel ((23), p. 44), to whom deference must be paid as a reliable observer, says that the follicle may attain a diameter of 10–20 mm. before it ruptures, and that no limits can be fixed to its growth within these figures; the test is whether the follicle contains a normal ovum. Testut ((31), p. 696), on the other

hand, is much more conservative in his estimate; he describes the follicle as usually measuring between 2 and 3 mm. or more, occasionally as much as 9 mm. As will be noticed, his upper limit falls below the lower value given by Nagel.

If it be that the larger figures, viz. 15 to 20 mm., are of common occurrence, it follows that the ovary in which such a follicle is found must present a remarkable appearance, since the size of the ovary itself is usually recorded as about 30 mm. in length, so that the presence of so large a follicle in its substance would very materially affect the surrounding tissue, and would greatly alter the external appearance of the organ.

It is possible that immediately prior to its rupture the Graafian follicle may undergo a sudden and rapid increase in its size, but so far, in the material at my disposal, I have not come across any follicles of the larger dimensions given, which in other respects could be regarded as normal.

Possibly deductions as to the size of the ripe follicle prior to its rupture have been made from the appearance displayed by the presence of corpora lutea in different stages of development, but in regard to this it may be observed, that we are without information as to the rapidity and extent of the changes that may ensue within the follicle immediately after its rupture.

In the accompanying table the results are given, so far as the size of the follicle is concerned, as observed in the material at my disposal.

Table I

Size of ripe Graafian Follicles containing Normal Ova

The measures are given in millimetres.

Specimen		Diameters	Distance from Surface
453 A	35*	1·63 × 2·00 × 1·96	0·3
01	122	4·53 × 3·14 × 4·90	0·3
453 B	14*	2·62 × 1·56 × 2·54	0·34
02	106	0·79 × 0·80 × 0·62	0·36
01	95	4·59 × 3·16 × 4·82	0·56
U 3	27	3·20 × 3·08 × 5·20	0·6
380	98**	1·47 × 1·84 × 2·80	0·88
453 A	3**	1·39 × 1·66 × 2·34	1·00
02	67	0·71 × 1·18 × 2·06	1·04
01	14	2·90 × 2·58 × 2·09	1·16
453 F	34	0·98 × 0·56 × 1·20	1·28
453 F	20	1·42 × 1·70 × 1·56	2·6
453 F	30	1·37 × 0·96 × 1·20	2·6

The specimens in this table are arranged in order of the thickness of the wall which separates the Graafian follicle from the surface of the ovary. Generally speaking, those with the thinnest wall are the larger follicles, though this is not an invariable rule, as may be seen from an inspection of the table. It would therefore appear that there is considerable variation in the size of the follicle independent of its proximity to the surface.

In specimens 453 B 14 and 453 A 35 (marked *) the contained ova, after

examination, have been pronounced mature. In specimens 453 A 3 and 380 98 (marked **), the contained ova are in the process of maturation.

Apparently the healthy Graafian follicle tends to be spherical, as if well filled. In cases where it is irregular in shape and angular in form the contents are generally found to be in a degenerated condition.

If the examples given in the above table are to be regarded as ripe for rupture, their relatively small size suggests that they are in a more or less quiescent condition, and that prior to their rupture they will undergo a sudden and more or less rapid increase in their bulk when the appropriate occasion arises. This is a matter which will be dealt with later in the paper.

Position of Cumulus

Another point on which there is much conflict of opinion, in the published accounts, is the position within the Graafian follicle of the cumulus or discus proligerus surrounding the ovum.

Nagel ((23), p. 57) very definitely states that "in man, and, as it seems, in most mammals (Waldeyer, Frey, Henle) the cumulus always has this position on the medial wall of the follicle, somewhat more to one side or the other of the middle line, and consequently always opposite the stigma (the point where the follicle ruptures)." This view is acquiesced in and followed by Poirier ((25), p. 695, vol. III.), Tigerstedt (32), and Piersol ((24), p. 1989).

McMurrich ((18), p. 19) qualifies it somewhat by stating that the discus is found "at one point *usually* on the surface nearest the centre of the ovary."

H. N. Martin ((20), p. 73) takes a diametrically opposite view, assigning a position to the cumulus usually corresponding to that "nearest the surface of the ovary."

A. Flint ((9), p. 759) expresses the opinion that "the situation of the discus proligerus is not invariable; sometimes it is in the most superficial and sometimes it is in the deepest part of the Graafian follicle."

Most authors maintain a discreet silence on the point, whilst J. H. Raymond ((26), p. 627) accepts the view of Böhm and Davidoff ((3), p. 352) to the effect that the discus proligerus with the contained ovum ultimately comes to lie free in the liquor folliculi, a change which is brought about by the softening of the cells forming the pedicle of the discus.

As the outcome of my own observations I feel justified in saying that the position of the cumulus or discus proligerus is not always on the deep wall of the follicle opposite the stigma, as stated by Nagel and others, but that in fact it may be frequently met with on the most superficial aspect of the follicle, i.e. that nearest the surface of the ovary, and consequently close to the stigma or point of rupture. Indeed, the position of the cumulus appears to be determined by no known law, and its occurrence on any part of the circumference of the follicle may be observed.

The view almost universally accepted, is that the discus proligerus remains throughout the growth of the follicle adherent to the cells of the stratum

granulosum through the medium of a pedicle which may vary considerably in appearance, in some cases being long and attenuated, in others short and wide. The appearance represented under the microscope will vary much according to the plane of section, and any satisfactory elucidation of the subject is only possible after the careful examination and reconstruction of serial sections.

It frequently happens that a single section, or, it may be, a small series of sections, would give support to the view that the discus proligerus with the contained ovum lay free in the liquor folliculi. On more extensive examination, however, so far as my own experience goes, these specimens can always be traced so as to reveal a connexion with the cells of the stratum granulosum. Such an observation, however, does not necessarily contravert the view taken by Böhm and Davidoff, for it is possible, as will be hereafter explained, that the cumulus and ovum may be found floating in the liquor folliculi, having acquired that position by a means other than that described by these authors, viz. the division of the pedicle.

The advantage of having the ovum and discus proligerus floating fairly free in the liquor folliculi is at once apparent when we come to discuss the mode and manner of the discharge of the ovum when the Graafian follicle ruptures.

It is obvious that the position of the cumulus must stand in some distinct relation to the mechanism which determines the escape of the ovum from the follicle.

If one accepts the view that the cumulus is always situated on that side of the follicle which lies farthest from the surface of the ovary, it becomes at once difficult to explain how it is possible, by any increase of pressure in the fluid contained within the antrum folliculi, for the ovum to be expelled through an aperture which lies on the opposite side to that on which it is placed. It seems more probable that the fluid pressure being equally exerted in all directions, is rather likely to force the ovum more firmly against the wall on which it rests. Hence the obvious advantage of a more superficial position as claimed by Martin (*loc. cit.*), for there the ovum resting on or in relation to the weakened wall of the follicle (stigma), where the rupture is about to take place, will naturally be expelled through the orifice made in the wall of the theca against which it lies, by the bursting pressure exerted by the liquor folliculi. Such an explanation seems feasible, and would be one way of explaining the escape of the ovum in those cases in which the cumulus is superficial in position. But the question naturally arises, is it the normal way?

In cysts which enlarge through the increasing amount of their fluid contents, there is a tendency towards the production of marked flattening of the cellular contents which line their more resisting envelopes. If this be the case, we would expect to find the cells of the stratum granulosum lining the interior of the follicle thinned and compressed, an appearance which we do not see; the absence of such a condition is probably to be accounted for on the supposition that these cells are really part and parcel of the liquor folliculi, forming

as it were a superficial layer of cells bathed in and surrounding the liquor folliculi, overlying, but not intimately attached to, the "basal membrane" or "external limiting membrane" of some authors (see Robinson (27) pp. 311 and 319) which lines the inner surface of the internal theca. It is on this layer that the pressure exercised by the contents of the follicle is apparently exerted, else, were the cells of the stratum granulosum a constituent part of the wall of the follicle, we would expect these cells, as already stated, to exhibit indications of the result of pressure. Reference will be made later to this basal membrane, meanwhile it will be sufficient to suggest that possibly there is a lymph space in association with it.

What holds good of the cells of the stratum granulosum must also apply equally to the cells of the cumulus. It would be natural to expect that in cases where the cumulus has a broad base and an absence of pedicle, the follicular cells of which it is composed would react to such pressure as may be exerted on them, were it not that they form a constituent part of the fluid and semi-fluid contents of the follicle. What is true of these cells would also apply to the ovum which they surround, consequently we are entitled to assume that all the contents of the follicle within the basal membrane are subject to an equality of pressure, whatever that pressure may be. For the present the consideration of this subject is postponed until certain other details of the Graafian follicle have been considered. Meanwhile I here place on record my own observations as to the position of the cumulus within the follicle.

In 15 Graafian follicles which might be accounted as "ripe," and having normal contents, the cumulus or discus proligerus was in seven cases situated superficially, that is towards the ovarian surface. In two instances it lay deep within the follicle, the term "deep" being here employed to indicate that the cumulus was placed on the wall of the follicle farthest removed from the surface of the ovary. In six follicles the cumulus lay to one or other side of the follicle, intermediate in position between the superficial and deep positions above indicated.

In 10 Graafian follicles either containing degenerate contents, or not so advanced in growth, the cumulus was situated six times superficially, twice laterally, and in two cases deeply.

These records are too few from which to deduce any reliable data, but are sufficient to contravert Nagel's statement, for out of 25 Graafian follicles the cumulus occupies a superficial position in 13 cases, or about 50 per cent. whereas it only occurs in the "deep" position, that accounted as normal by Nagel, in four instances or 16 per cent.

Liquor Folliculi

Concerning the manner of the production of the liquor folliculi there is much divergence of opinion. The question at issue is whether the liquor folliculi is of intercellular or intracellular origin.

Scattered among the follicular epithelium, contained within the Graafian

follicle, are certain structures called the bodies of Call and Exner (4). These have been variously interpreted, by some as vacuolated cells (the "epithelial vacuoles" of Flemming ((8), p. 378)), by others as intercellular collections.

The prevalent ideas with regard to the origin of the liquor folliculi may be briefly stated as follows. Nagel ((23), p. 54) regards it as formed partly by transudation from the vessels surrounding the follicle, partly by disintegration of the large follicular cells (the "bodies of Call and Exner" or the "epithelial vacuoles" of Flemming), whose protoplasm swells, finally to be completely broken up, the nucleus at the same time crumbling away and finally breaking up.

On the other hand C. Honoré ((14), p. 537), from his researches on the rabbit, states that the stratum granulosum secretes the liquor folliculi just as the epithelium of the tubes of the kidney secretes urine. He explains the presence and appearance of the bodies of Call and Exner as follows. A certain number of the cells of the stratum granulosum group themselves radially and *secrete* a substance at first homogeneous. This central substance later becomes a reticulum, and increases in size with the growth of the follicle; the reticulum becomes finer, and a kind of peripheral membrane appears, at the same time the radial arrangement of the surrounding cells becomes less evident. The staining of these bodies in follicles of different sizes shews that their chemical constitution is modified by age.

My own observations on this subject may best be explained by a series of microphotographs, which I venture to think illustrate the successive stages of the process.

The feature which enables the observer to recognise them consists in the arrangement, in radial fashion, of the follicle cells disposed around them. This appearance is so characteristic that Call and Exner suggested that they were of the nature of ova, and that the arrangement of the cells surrounding them was comparable to the corona radiata encircling the ovum.

Within the area circumscribed by this radial formation of the follicular cells, in a typical example, there is a mass of variable size, often of a more or less clear, homogeneous matter, reacting to some stains in a selective way, but generally presenting appearances which correspond in tint and density with the reaction to the same stain of the coagulum in the antrum folliculi. The nature of the material occupying the centres of these radially arranged follicular cells has been variously interpreted. By some, these "bodies" have been regarded as the product of the liquefaction of the protoplasm of the follicular cells (Nagel (22), p. 381; Waldeyer (34), p. 38). Bernhart considered them of a fatty nature, but this view was combated by Bischoff, who held that they failed to refract the light sufficiently to justify this assumption. Flemming describes them as vacuoles of epithelial origin. C. Honoré regards them as having an intercellular origin and as being due to the accumulation of the products of the special activity of the radially arranged follicular cells around them.

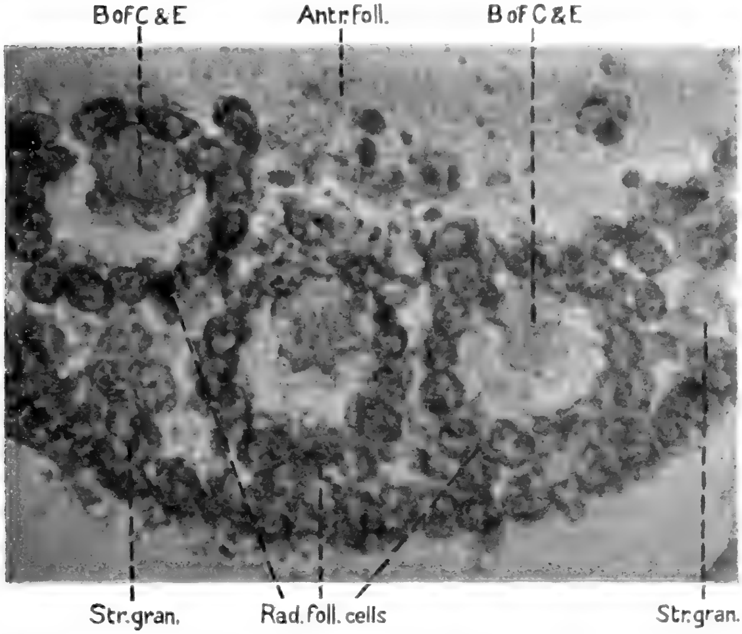

Fig. 1. Shewing bodies of Call and Exner (B. of C. and E.) surrounded by radial arrangement of follicular cells (*Rad. foll. cells*) in the stratum granulosum (*str. gran.*) of a human Graafian follicle. × 900 diameters. *Antr. foll.* antrum folliculi. Specimen 280 G. 5.

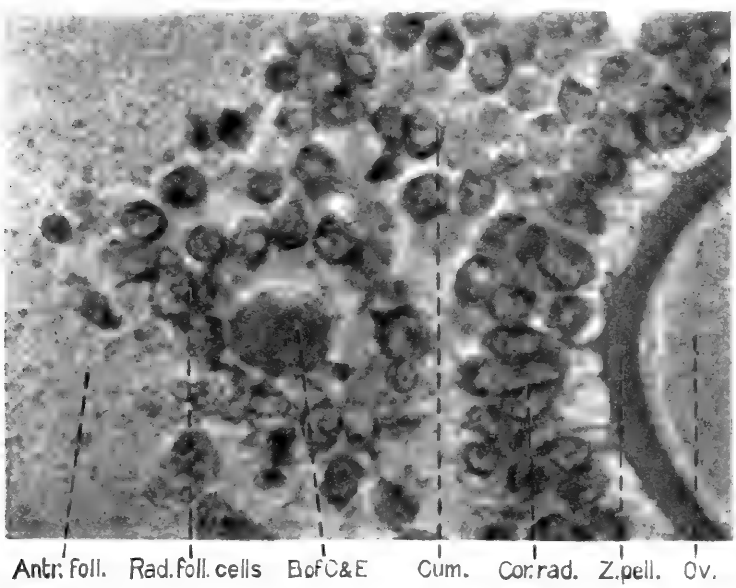

Fig. 2. Shewing a body of Call and Exner (B. of C. and E.) surrounded by radial arrangement of follicular cells (*Rad. foll. cells*) in the cumulus (*cum.*) of a human Graafian follicle. × 900. *Ov.* ovum.—*Z. pell.* zona pellucida.—*Cor. rad.* corona radiata.—*Antr. foll.* antrum folliculi. Specimen 280 G. 4.

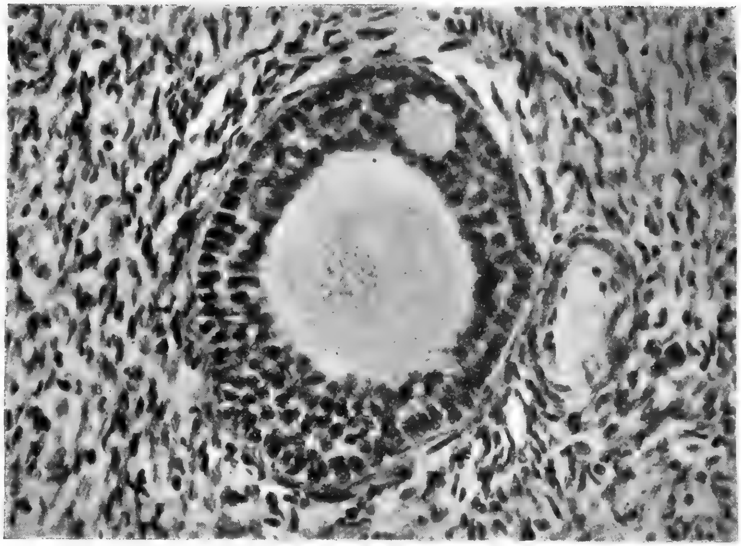

Fig. 3. Ovum within the stroma of the ovary surrounded by follicular cells. As yet there is no antrum folliculi. Near 1 of the watch dial there is a body of Call and Exner surrounded by a corona of follicular cells, within which the structure presents a homogeneous appearance. ×400. Specimen O. 2. 59. 4.

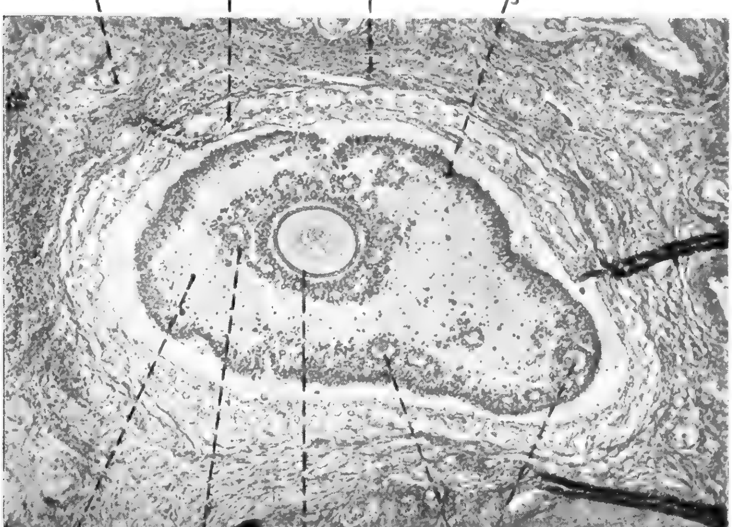

Fig. 4. Section of a human Graafian follicle containing a maturing ovum. *Ov. str.* ovarian stroma; *Int. theca,* internal theca; *ext. theca,* external theca; *str. gran.* stratum granulosum; *antr. foll.* antrum folliculi; *cum.* cumulus, with bodies of Call and Exner therein; *ov.* ovum; surrounded by zona pellucida and corona radiata. B. of C. and E., Bodies of Call and Exner in the stratum granulosum. ×100. Specimen 280. G. 2.

In attempting an elucidation of these various views it will be necessary to draw attention first to the stage at which these bodies make their earliest appearance, and the manner of their distribution.

Fig. 3 represents the appearance of one of these bodies as seen in a Graafian follicle in which there is as yet no antrum folliculi. In the specimen shewn, the body of Call and Exner is of large size as contrasted with others which occur in the serial sections of the same follicle, and its contents react to the stain (iron haematoxylin and Van Giesen) in such a manner as to be coloured a deep orange. It may be noted that in follicles in which an antrum folliculi occurs, under the same staining reagents the enclosed coagulum is usually tinted yellow. The same relation is seen in specimens stained with Mallory's connective tissue stain, both coagulum and "bodies" are coloured blue, the latter much more deeply. This circumstance would suggest that the liquor folliculi is of the same or similar nature as the matter contained in the bodies of Call and Exner, though possibly more dilute.

The question of size, to which reference has been already made, is a matter of some importance, as will presently be noted, as having a bearing on the manner of formation of these bodies.

In regard to their distribution. As stated above, they occur in follicles prior to the formation of the antrum folliculi, and I have seen evidences of what I took to be their genesis in follicles as early as the double-layered stage of the follicular epithelium. Subsequent to the appearance of the antrum folliculi, they are met with equally amongst those parts of the follicular epithelium which are ultimately to become the stratum granulosum, and in the cumulus, as shewn in fig. 4.

When, however, by the increase in the size of the antrum folliculi, the stratum granulosum becomes much thinned, then we find their occurrence in that layer much less frequent, until in advanced stages of the growth of the follicle they cease to be met with in the stratum granulosum altogether.

Not so, however, in the region of the cumulus, for here, immediately around the ovum and towards the basal part of the cumulus, they may be seen in follicles which are to be regarded as near approaching rupture, to judge by the thinness of the superficial wall and the mature condition of the oöcyte.

Meanwhile it may be noted that these so-called bodies of Call and Exner, in different stages of their development, exhibit very different appearances.

I am fortunate in being able to reproduce a microphotograph of the appearances displayed in the basal region of the cumulus where that structure becomes continuous with the stratum granulosum. Here within the same field certain appearances are to be noted which very definitely suggest that these bodies are the result of changes actually taking place in single follicular cells, or, it may be, in groups of such cells (fig. 5).

Fig. 6 is a view shewing in the centre of the field a follicular cell which is remarkable on account of its size and appearance.

Enclosed within a definite cell wall the cytoplasm appears uniformly granu-

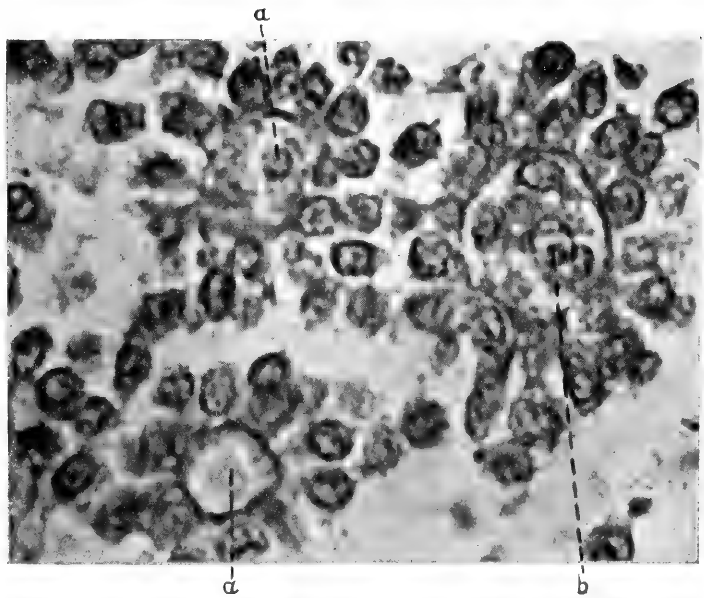

Fig. 5. Section through the base of the cumulus of a human Graafian follicle shewing three bodies of Call and Exner (*a*, *a*, *b*). Two of these (*a*, *a*) are seen to be formed from single follicular cells, whilst *b* exhibits their origin from a group of follicular cells. ×900. Specimen 280. 12. 5.

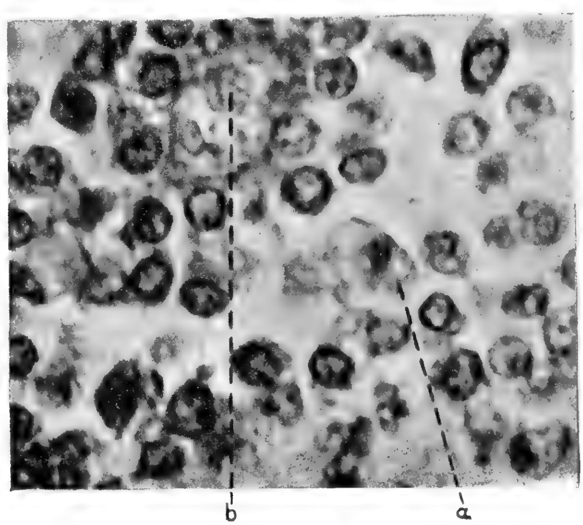

Fig. 6. Section through the follicular epithelium shewing *a* an enlarged follicular cell prior to its being surrounded by a corona of contiguous follicular cells. At *b* a similar follicular cell is seen in process of being so surrounded. ×900. Specimen 453 A. 4. 5.

lar, and stains somewhat more deeply than that of the surrounding cells; within this the nucleus shews up as a darker mass with no clearly defined nuclear membrane such as is so characteristic of the surrounding cells, and the chromatin granules are no longer isolated, but appear to be diffused through the nuclear protoplasm (karyoplasm) in such a way as to impart a darker tint to the whole nuclear substance, evidently a stage in the ultimate dissolution of that structure.

In fig. 7 a further stage is exhibited. Here there is distinct evidence of a vacuolation of the cytoplasm taking place within the cell membrane, while the nucleus becomes less distinct and seems to be more diffuse. At the same time, as will be seen in the figure, the surrounding follicular cells, by the increasing

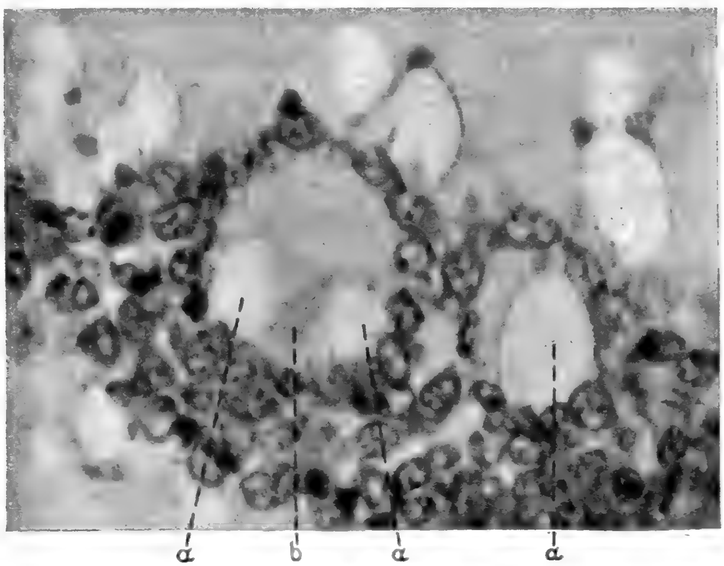

Fig. 7. Section shewing vacuolation of cells composing bodies of Call and Exner, *a*, *a*, *a*. At *b* the nucleus of one of them is disappearing. ×900. Specimen 280. 16. 5.

expansion of the central cell undergoing these changes, arrange themselves in radial fashion, as would naturally be expected under the circumstances. In the same field another such body is seen enclosed in typical fashion by the characteristic radial formation of the surrounding follicular cells, though here a large vacuole occupies the major part of the cell and the nucleus has disappeared.

The occurrence of the vacuolation seems to vary in different examples; in many this phenomenon does not occur till after the nucleus is completely dissipated within the substance of the cell, so that the central mass produced would seem to form a more or less homogeneous, seemingly solid, clearly staining material, occupying the centre of the radial formation of the follicular cells. The change in the subsequent appearance of this substance is effected through

Fig. 8. Section shewing the body of Call and Exner now reduced to the form of a reticulum by the vacuolation of its substance. Around the vesicle so formed the contiguous follicular cells are grouped in coronal fashion. ×900. Specimen 453 A. 4. 5.

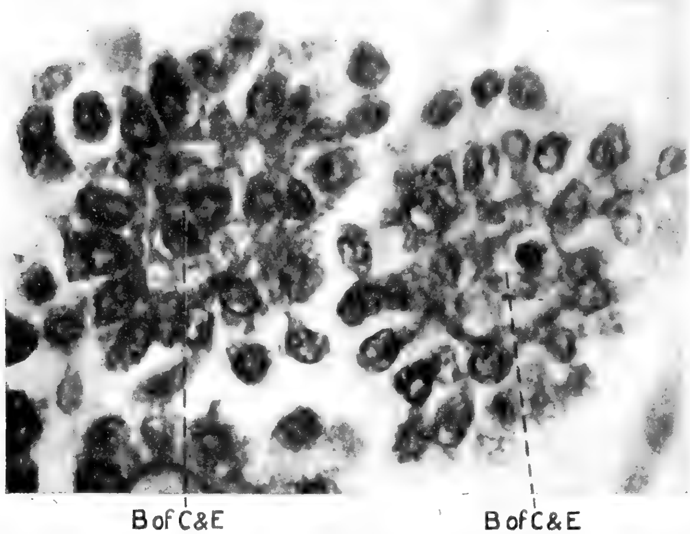

Fig. 9. Section shewing how the bodies of Call and Exner (B. of C. and E.) may be compounded of a number of follicular cells. ×900. Specimen 453 A. 4. 5.

the appearance either at the side of, or within it, of vacuoles of different sizes. In the first instance these spaces may be small and few, in which case the appearance presented is that of a coarse reticulum. In other cases the central mass may be transformed into a fine reticulum by the presence of a number of vacuoles which break it up in a more effective way, as seen in fig. 8.

Hitherto we have assumed that these appearances are the result of the changes induced in one follicular cell, but there is evidence that groups of cells may be agglutinated together, becoming, so to speak, encapsuled to form the centre of a radial formation, thereby greatly increasing the size of the so-called "body of Call and Exner." Fig. 9 represents this appearance.

The individual cells of these groups appear to undergo the same changes as those noted in the single cells already referred to, resulting in the fusion

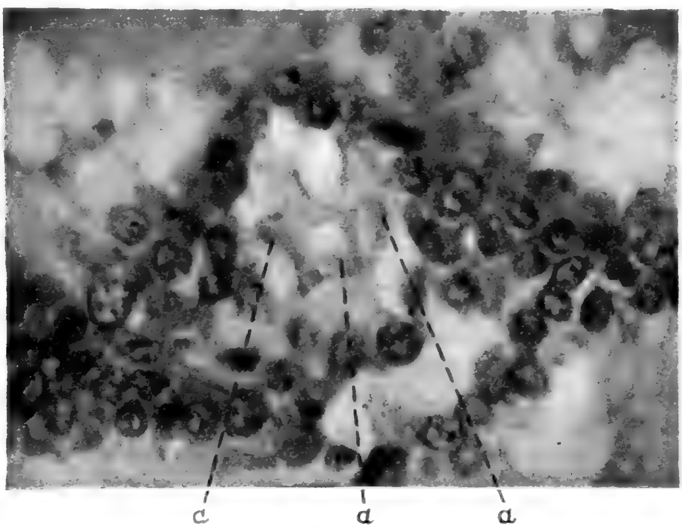

Fig. 10. Section of a body of Call and Exner vacuolated and shewing the disappearing nuclei, *a*, *a*, *a*, of some of the cells of which it is compounded. × 900. Specimen 280. 12. 5.

of their products, and displaying this difference, that the size of the resulting body is considerably larger, and the reticulum more complex.

A further proof of this is seen in fig. 10, where there is distinct evidence of the presence of nuclear structures within the resulting reticulum.

The microphotographs here reproduced make it clear that the bodies of Call and Exner can in no sense be regarded as due to the accumulation of the products of the special activity of the radially arranged follicular cells around them, as suggested by Honoré, but must be interpreted as the result of changes in a follicular cell or group of cells, whereby modifications are induced in their molecular structure, leading to the production of certain materials at different periods of their dissolution, and ultimately resulting in a liquefaction of the

bulk of their contents, which, together with a residual stroma, contributes to the increase in the amount of the liquor folliculi.

In this respect my observations lead me to support the view advanced by Nagel and others. There can, I think, be little doubt but that the radial arrangement of the surrounding follicular cells is a purely mechanical result, and that the so-called bodies of Call and Exner are merely to be considered as foci of the processes which ultimately result in the breaking down of the primarily compact mass of follicular cells, coincident with the production of an antrum folliculi and the subsequent distension of that cavity with fluid.

In this way the major part of the follicular cells disappears. As to how they are replaced or multiply, we have the evidence of Flemming ((8), p. 376 and pl. XIX, figs. 32–34), who describes the frequent occurrence of karyokinetic figures in the cells of the stratum granulosum of the cat and the rabbit, and of Harz ((12) p. 374) who records mitosis in the follicular cells of the mouse, whilst Nagel ((22) p. 379, pl. XXI, fig. 14) refers to it as demonstrated in the human female.

In Professor A. Robinson's memoir (27) I note the occurrence of mitotic division as exhibited in his beautiful series of microphotographs (see fig. 58, pl. X).

It follows that subsequent to the disappearance of the bulk of the follicular cells, only a thin layer of cells, often only a single row in thickness, is left lining the inner surface of the internal theca, and over-spreading the external limiting membrane. This much reduced layer constitutes the stratum granulosum.

The only other situation in which the follicular cells appear to persist is in the region of the cumulus, where in nearly all advanced Graafian follicles they remain as a stalk or pedicle to the mass of cells which contains the ovum.

In these situations the follicular cells which may subsequently undergo liquefaction, if this term may be employed, are not bedded in a compact mass of surrounding cells, but often lie in such a position that one part of their surface is only covered by a single layer of follicular cells, or may lie free in the wall of the antrum folliculi. The first of these conditions is represented in fig. 11, where in the stratum granulosum the body comparable to that of Call and Exner is represented by the cyst-like formation, the wall of which, directed to the antrum folliculi, is formed of a thinned and spread-out layer of follicular cells.

Fig. 12 shews the changes presented by a follicular cell superficially placed, i.e. one of the cells lining the antrum folliculi. Here, within a vacuole, the contained nucleus is exhibited undergoing evident dissolution. Similar changes are also represented in fig. 13, in which case the change in the appearance of the nucleus within the vacuole is less marked.

It would seem, in some cases, that the nuclear elements do not entirely disappear, a fact which would account for the presence in the liquor folliculi of the numerous nuclear-like bodies not unfrequently met with.

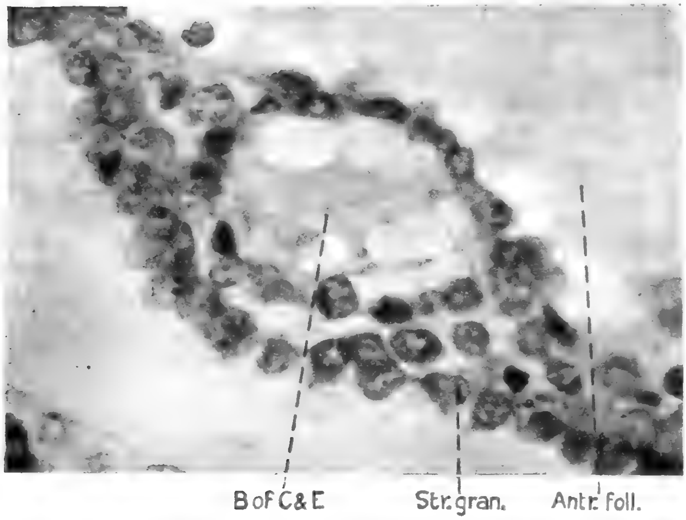

Fig. 11. Section of a body of Call and Exner in the stratum granulosum (*str. gran.*) separated from the antrum folliculi (*antr. foll.*) by but a single layer of follicular cells. × 900. Specimen 280. 12. 5.

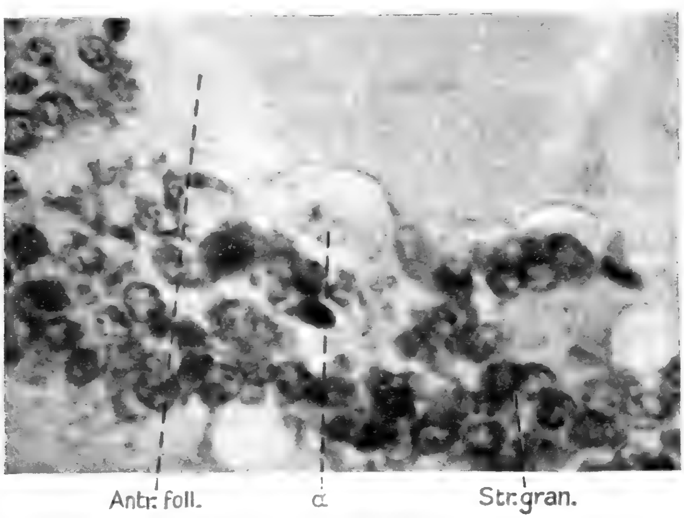

Fig. 12. Section shewing a follicular cell, *a*, of the stratum granulosum (*str. gran.*) undergoing dissolution. The nucleus is seen in an altered condition surrounded by a vacuolated space which may either be an artefact of the nature of a retraction cavity or may contain fluid of a different chemical constitution from that contained within the antrum folliculi (*antr. foll.*) which is seen in the form of a coagulum. × 900. Specimen 280. 16. 5.

In considering the changes in the follicular epithelium coincident with the appearance and expansion of the antrum folliculi, a staining reaction which is by no means infrequent must be here referred to. This consists in a marked difference with which some of these follicular cells react to the same stain, or combination of stains. It is best seen in the specimens which have been subjected to the influence of some such reagent as Mallory's connective tissue stain, whereby some of the cells become stained of a pink or a yellow colour, as contrasted with others (the majority) which exhibit a blue tint, an occurrence which would suggest that some of the cells were undergoing a change in their chemical constitution.

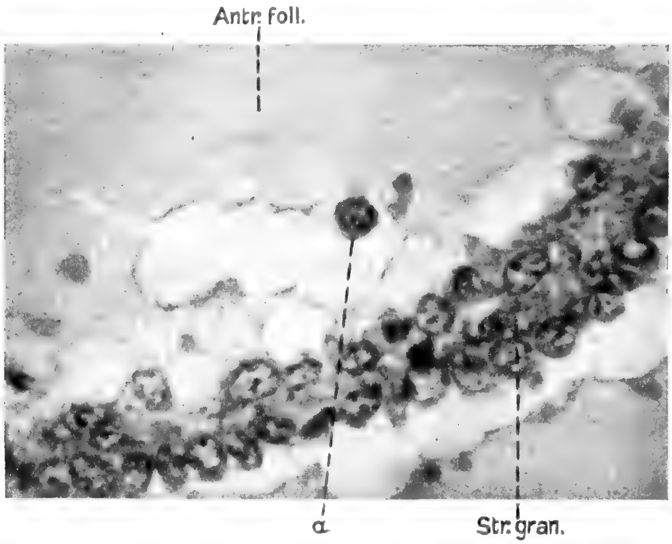

Fig. 13. Section shewing stratum granulosum (*str. gran.*) with a separated follicular cell (*a*) lying within a vacuolated space within the coagulum occupying the antrum folliculi (*antr. foll.*). The separated follicular cell (*a*) does not as yet present any appearance of undergoing change. The vacuole around it may be an artefact or due to the vital activity of the cell (*a*). ×900. Specimen 280. 14. 4.

It has been said that the cells of the stratum granulosum lining the interior of the follicle and resting on the membrana limitans externa which separates them from the inner surface of the internal theca, although often reduced to a single row of cubical cells, yet exhibit no appearance of flattening or compression, such as would be due to the result of pressure from within; for this reason these cells must be regarded as a constituent part of the contained liquid contents of the follicle, the pressure exercised by which is supported by the internal theca overlain by the membrana limitans externa.

Another matter to which attention must be incidentally directed is the fact that the stratum granulosum is exceedingly prone to separate from the inner theca of the follicle. In this connexion the observations of Robinson ((27), p. 320) on the ovarian follicles of the ferret are of interest. After pointing out

that Wagener, Schottländer, and Limon regard the membrana limitans externa as a connective tissue structure, whilst Waldeyer and Nagel believe that it is formed by the follicular cells, the latter asserting that it is similar at first to the oölemma, Robinson proceeds to point out that in the ferret, the membrana limitans externa does not react to stains in the same way as does the oölemma (zona pellucida), and that when the follicular epithelium is detached from the internal theca by the action of the fixative reagents, the membrana limitans externa separates into two layers, as displayed in the figures he gives (figs. 58 and 60, pl. X). "The inner of the two layers," continues the author, "is connected with the outer ends of the follicle cells, and is possibly formed by them in the same way that the external limiting membrane of the central nervous system is formed by the outer ends of the neuroglial cells. The outer layer is connected with the innermost flattened cells of the internal theca, and it reacts like other connective tissue structures to connective tissue stains." He says further "Its function is unknown, but its constant presence indicates utility, and it possibly regulates the passage of different materials in opposite directions to and from the follicle."

In regard to the staining affinities of the membrana limitans externa and the zona pellucida in human material, our own observations do not correspond with those of Robinson. In general, allowing for the difference in the density of the two structures—the membrana being exceedingly delicate as compared with the zona—the staining reaction appears to be very similar—both take up the plasma stain as distinct from the nuclear stain. The appearance of the membrana limitans externa is in every case very similar to that of the capillary walls, in fact of all vessels which possess no muscular coat.

In sections of the rabbit's ovary, which were examined after being subjected to Mallory's connective tissue stain (fixative: Flemming's (strong) formula), both the zona and the membrane were tinted blue alike. It was noticeable that in the rabbit the membrane was a somewhat denser layer than is revealed in the human Graafian follicle.

Observations on the human material at my disposal confirm the view that the cells of the stratum granulosum are very prone to separate from the inner surface of the internal theca of the follicle, and when this separation takes place, the layer which intervenes, viz. the external limiting membrane, invariably remains attached to the connective tissue elements of the internal theca. The separated layer of the stratum granulosum exhibits little appearance on its outer surface of any but the feeblest connexion with this membrane, and in most cases shews little evidence of any connecting fibres. In some instances it would appear as if the union between the stratum granulosum and the membrana limitans externa was sufficiently intimate to lead to a tearing away of a layer of this latter structure, along with the cells of the stratum granulosum, so separating it into two layers, as described by Robinson, the inner being connected with the outer surface of the cells of the stratum granulosum, the outer still remaining adherent to the inner surface of the internal

theca, though no difference in staining reaction such as is described by Robinson could be discerned. The accompanying figures (figs. 14 and 15) represent both conditions.

The fact that the ease with which the stratum granulosum appears to separate from the membrana limitans externa seems to vary with the ripening of the follicle, would suggest that this separation is a natural process, and not necessarily an artefact as frequently supposed. The fact, too, that the membrana limitans externa is at times prone to split into an external and an internal layer, where separation of the stratum granulosum takes place from the inner surface of the internal theca, inclines one to the view that possibly this intervening layer between these two mentioned structures may be in fact permeated by an irregular lymph space, which weakens the bond between the internal theca and the layer of the contained follicular cells, and so renders more easy the separation of the two structures. For apart from the evidence forthcoming in the examination of unruptured follicles, there is the circumstance that immediately after the bursting of the follicle and prior to the formation of a corpus luteum, the entire stratum granulosum is shed and disappears, leaving only the internal theca and the membrana limitans externa lining it. Moreover, through the courtesy of Professor Robinson I have been able to note the fact that in the ferret the ovum after it has escaped from the Graafian follicle is not only surrounded by the cells of the cumulus, but also has connected therewith a considerable amount of a layer corresponding to the stratum granulosum, thus proving that at the time of rupture the stratum granulosum was in part or in whole discharged. These observations seem to point to the separation of the stratum granulosum from the internal theca as a normal process, and not necessarily an artefact as so many hold it to be.

This matter will be again referred to when the mode of rupture of the follicle is discussed.

In concluding this section relating to the liquor folliculi, mention must be made of the varieties of coagulum met with in the follicle, even when subjected to the same fixing reagent. In many instances the coagulum exhibits the appearance of fine ground glass, in others the granulations are coarser. In some it takes on the form of an open meshwork. In all, as best seen at the edges, the reticulum varies much in appearance, in some it is fine, in others, coarse. These appearances, met with in what seem normal follicles, combined with the variety of tint displayed when subjected to the same staining reagent, suggest that the physical and chemical constitution of the liquor folliculi is not always constant, but is undergoing change, it may be by the addition or subtraction of constituents which affect its density or alter the character of its composition.

The Sheath of the Follicle

As usually described the specialised part of the ovarian stroma around the follicle consists of two not very clearly defined zones, the internal theca and

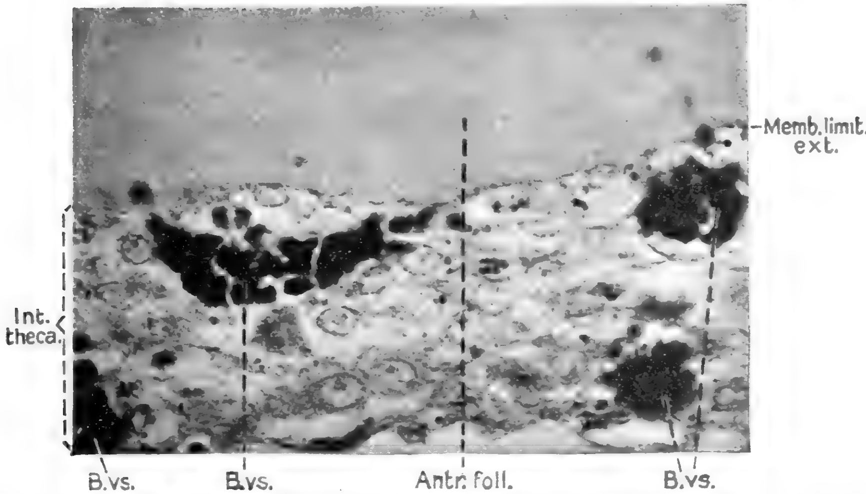

Fig. 14. Section shewing the appearance of the internal theca (*int. theca*) when the stratum granulosum has become separated from it. The membrana limitans externa (*mem. lim. ext.*) is seen adherent to the internal theca. *B.vs.* capillaries within the internal theca filled with blood corpuscles. × 700. Specimen O. 1. 103

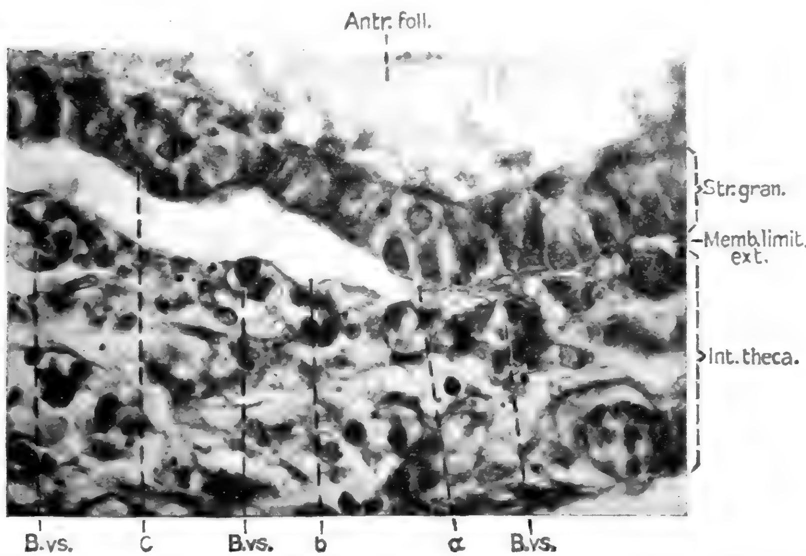

Fig. 15. Section of the wall of a follicle shewing stratum granulosum (*str. gran.*) and internal theca (*int. theca*) lying in apposition, with the external limiting membrane (*mem. lim. ext.*) in between; at the point *a* this layer is seen to split, one layer (*b*) adheres to the internal theca, the other (*c*) clings to the stratum granulosum; the interspace between is probably a lymph space. *B.vs.* capillaries of internal theca: *antr. foll.* antrum folliculi. × 600. Specimen O. I. 20. 5.

the external theca. The internal theca is composed of a loose cellular stroma made up of round and spindle-shaped cells, and has a capillary net-work throughout its substance. To the outer side of this lies the external theca, in which zone, the tissue is denser, more fibrillar, and less vascular, though here the blood vessels are larger, and furnish the branches which supply the capillary plexus of the internal theca. In the theca externa there are also described a number of hollow spaces which are interpreted as enlarged lymph channels.

A study of the appearance of the internal theca reveals the fact that this layer becomes richer in capillaries as the growth of the follicle proceeds (see Nagel, (23), p. 56); so also the round cells become larger and more numerous. In some instances I have reason to believe that the theca interna over the area which corresponds to the site of the cumulus is more vascular than in other parts of the circumference of the follicle, a fact which, as will presently appear, has some significance.

Not only does the internal theca appear to be richer in capillaries, but in several instances, one of which is here represented (fig. 16), the capillaries are not confined to the theca interna, but invade the substance of the follicular epithelium, where it forms the base of the cumulus or discus proligerus.

So far as I am aware, no mention of this condition has hitherto been made, and I was inclined to regard the first specimen I observed of this appearance as of the nature of a haemorrhage. The sections, which were stained with Mallory's connective tissue stain, revealed the blood corpuscles as tinted a brilliant scarlet, a feature which enabled us to trace with ease their disposition and arrangement. By adopting a method of reconstruction it was possible to prove the continuity of these collections of blood corpuscles, and to trace their connexion with the capillaries of the internal theca; there was also distinct evidence that around these collections of blood cells there was a delicate membrane, directly continuous with, and presenting the same appearance as, that enclosing the capillary channels of the internal theca. Obviously it was hazardous to base any conclusion regarding the nature of this condition on its occurrence in one particular specimen, consequently a search was made to see whether it occurred in other follicles. The result was confirmatory, for in several other instances the presence of blood corpuscles similarly grouped and ensheathed was clearly demonstrated, though it must be admitted, that but for the differential staining produced by the employment of Mallory's formula the occurrence of this particular arrangement might have been overlooked.

On reviewing the evidence, however, it was particularly noticeable that, with one exception, all the specimens exhibiting this feature were derived from the same source, a woman who died of heart disease, and regarding the post mortem of whom the report records the occurrence of "back pressure" changes in many of the viscera. This condition may naturally be regarded as answerable for the appearance displayed, and might be accepted as conclusive evidence that the arrangement of the capillaries represented is abnor-

mal, were it not for the fact that a similar condition was met with in the ovary of a woman aged 35 who died of laudanum poisoning, in which case the ovum contained within the follicle was degenerate. It may be that the administration of this drug is alike responsible for the unusual appearance observed. Whatever be the cause, and whether or no we are to regard the incidence of

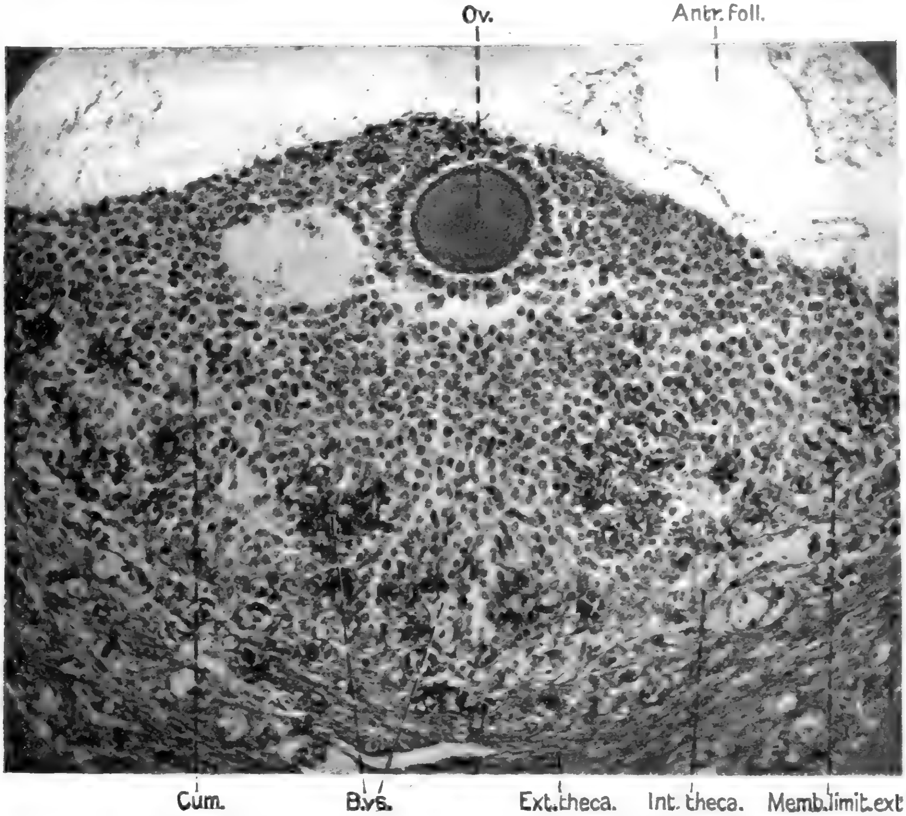

Fig. 16. Section through the cumulus of a human Graafian follicle shewing ovum *in situ* surrounded by the zona pellucida and corona radiata. The base of the cumulus is invaded by capillaries containing blood cells. These are seen to be enclosed by distinct walls similar to those displayed by the capillaries of the internal theca (*int. theca*). The membrana limitans externa (seen at *mem. lim. ext.*) seems to disappear as a definite layer in the region corresponding to the base of the cumulus (*cum.*). *Ext. theca*, external theca; *antr. foll.* antrum folliculi. ×200. Specimen 453 F. 20. 4.

this feature as normal or abnormal, its occurrence is worthy of record, since possibly, if normal, it may be the means of providing the ovum with an increased source of nutrition, whilst if abnormal, it may account for degenerative conditions which may arise in like or similar circumstances.

It is interesting to note that in the specimens taken from the woman who died of heart disease, the presence of this condition did not appear to have any

deleterious effect on the ova, for in the sections examined these appeared to be normal. In the case of the woman who died from laudanum poisoning it is open to doubt whether the degenerated ovum was a direct result of the poison or secondary to the vascular changes present.

There arises in this connexion the question of the relation of the membrana limitans externa (basal membrane) to these capillary invasions. It would appear from an examination of the specimens in which this peculiar distribution of the vessels occurs, that in the neighbourhood of their entry into the cumulus the membrana limitans externa has disappeared, and there seems no line of demarcation to separate the follicular cells from the connective tissue elements of the theca interna.

It must not be assumed that the cases I have recorded include all the instances of blood within the follicle. Not unfrequently undoubted cases of haemorrhage are met with, occurring either as scattered masses of blood corpuscles within the substance of the follicular cell work, or else discharged in bulk into the antrum folliculi. These collections we generally found associated with molecular changes in the walls of the follicle, and also combined with marked degenerative changes in the ovum itself. It may be that the appearances I have noted, and here figured, are only an early stage of the process which ultimately results in a diffuse haemorrhage. If so, they may be of interest as shewing how this destructive process leading to the atresia of the follicle is induced.

Of the changes which take place in the structure of the internal theca at the point corresponding to the site of its ultimate rupture little need be said. As the covering wall of the follicle in this region becomes thinner its vascularity becomes reduced.

Already reference has been made to the membrana limitans externa (basal membrane). This, as has been said, intervenes between the inner surface of the theca interna and the peripheral cells of the follicular epithelium which lie within the follicle. It is shown *in situ* in fig. 17.

As already described, when separation occurs between these two constituents of the follicle, the bulk of the membrana limitans externa (basal membrane) remains adherent to the flattened cells forming the inner surface of the internal theca (see fig. 14). For this reason, the term "basal membrane" as applied to it, suggesting its intimate connexion with the cubical cells of the stratum granulosum which overlie it, is misleading. Its behaviour and anatomical disposition are more in accord with the interpretation of the term "external limiting membrane" applied to it.

It should be noted that in many parts of the section of the wall of the follicle this limiting membrane is the only layer which intervenes between the capillary stream and the contents of the follicle, and if so be, as has been suggested by its tendency to split into two layers, this limiting membrane contains a series of lymph channels within its substance, it may well be that it forms a structure of no little importance, not only in regard to the nutrition

of the follicular contents, but also in connexion with the process involving the rupture of the follicle itself.

The external theca. As already explained, there is no clear line of differentiation between this and the internal theca; it differs from the latter in the absence of a capillary network, and the greater density of its constituent layers, which are largely composed of fibrillar tissue, derived from the surrounding ovarian stroma, and concentrically arranged around the Graafian follicle. It is to the nature of this tissue that attention must first be directed.

Schäfer ((29), p. 643) thus describes the ovary: "Each ovary is formed of a solid mass of fibrous-looking tissue (stroma), which contains between its fibres

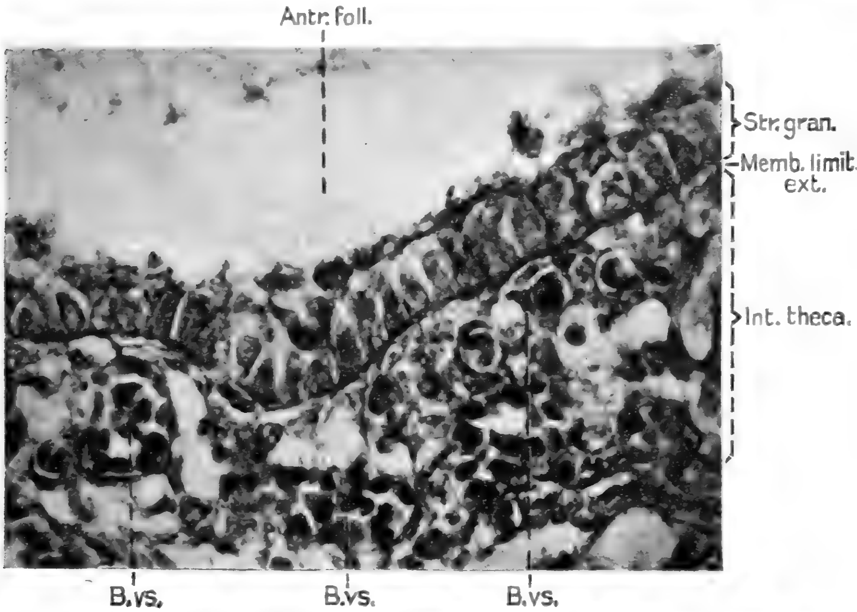

Fig. 17. Section through the wall of a human Graafian follicle shewing stratum granulosum (*str. gran.*), membrana limitans externa (*mem. lim. ext.*) and internal theca (*int. theca*) all in contact. *B.vs.* capillaries of internal theca containing blood. *Antr. foll.* antrum folliculi. ×700. Specimen 453 B. 27. 3.

very many elongated cells like those of embryonic fibrous tissue...Along the line of attachment (hilum) blood vessels and nerves enter and leave the ovary, and accompanying these is a strand of fibrous tissue which contains plain muscle amongst its fibres."

Piersol ((24), p. 1987) says of the cortex of the ovary: "The stroma cells somewhat resemble the elements of involuntary muscular fibre in appearance," and in reference to the medulla says it consists of fibro-elastic tissue and smooth muscle accompanying the larger vessels. In this connexion it may here be stated that in a specimen stained with Weigert's elastic tissue stain the only situation in which elastic fibres were recognised was in relation to the walls

of the vessels—neither in the general stroma of the organ nor in the follicular walls was there any evidence of the presence of elastic tissues.

Nagel ((23), p. 49) states that in the zona vasculosa there is "an extension from the muscular tissue of the broad ligament along the larger vessels, better marked in mammals than in man."

It would seem, therefore, that in the groundwork of the ovary we have to deal with fibrous and muscular elements, the differentiation of which is not always an easy matter.

Winiwarter ((35) and (36)) states that the distribution of the muscular element in the human ovary is identical with that exhibited in the cat, in which

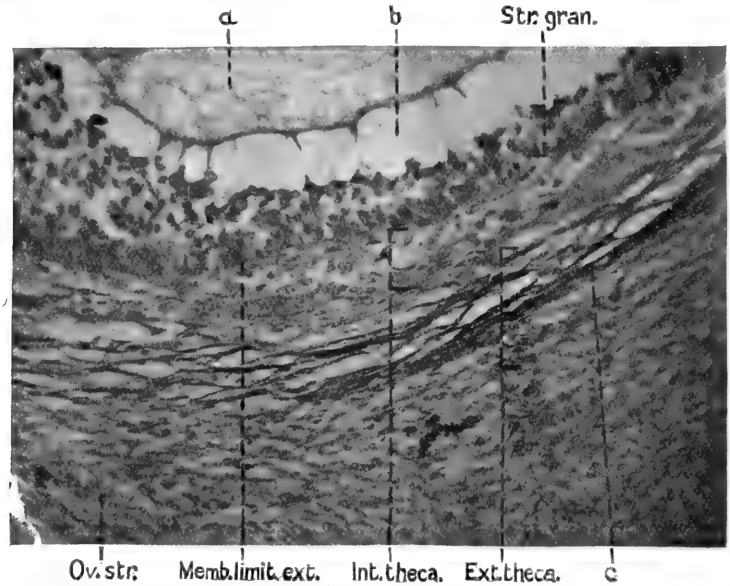

Fig. 18. Section through the wall of a human Graafian follicle. *a*, coagulum within antrum folliculi; *b*, retraction space between coagulum and stratum granulosum (*str. gran.*); *int. theca*, internal theca with capillaries; *ext. theca*, external theca with (*c*) bundles of smooth muscular fibre differentially stained with safranin and light green. ×400. Specimen O 2. 52. 3.

animal he describes it as entering into the formation of the external theca of the Graafian follicle. Before I was acquainted with his conclusions I was myself engaged in analysing the nature of the fibres of the external theca, and had been led independently, through the staining reactions, to suppose that all the fibrils were not of a like nature.

My attention was first directed to this whilst examining some specimens stained with safranin and light green. With this reagent some of the concentric fibres of the external theca were stained a pronounced pink, which stood out in contrast to the grayish green tint of the surrounding stroma. Fig. 18 exhibits the appearance in a section through the follicular wall.

The coagulum within the antrum folliculi is stained a bright green in the

original specimen, the membrana granulosa is purplish in tint. The theca interna is coloured a purplish gray, whilst in the theca externa there are elongated fibres which, staining a pronounced pink, stand out in marked contrast to the surrounding grayish green stroma. Confirmatory evidence was

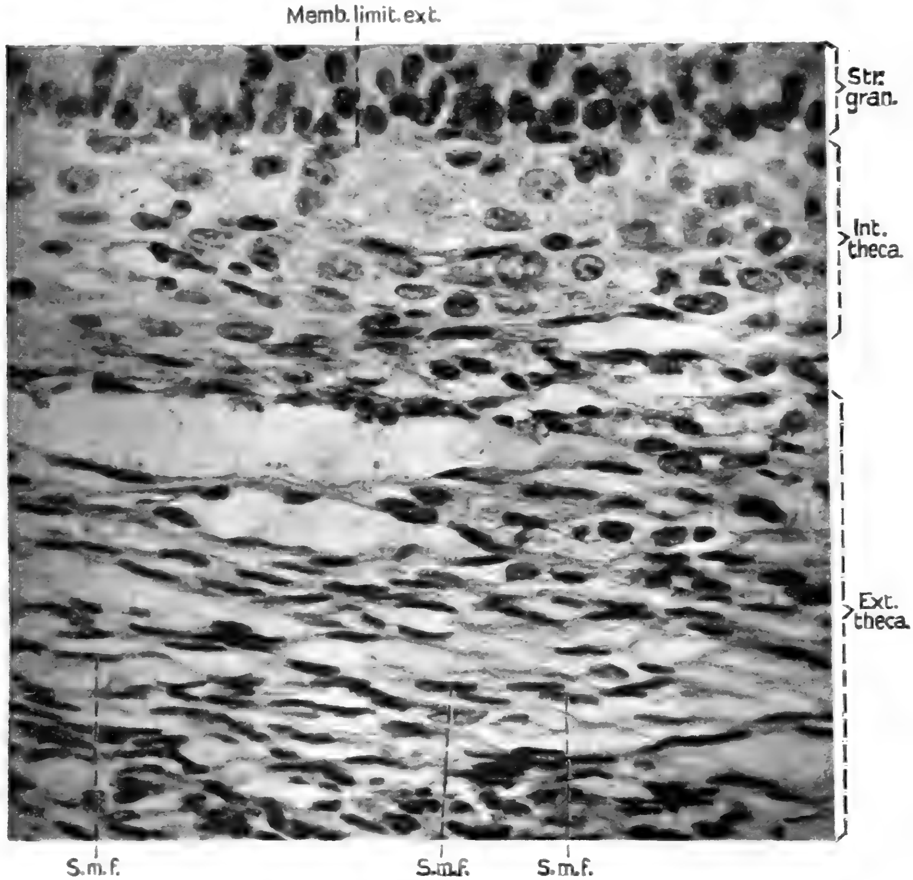

Fig. 19. Higher magnification of a portion of the same follicular wall as that shewn in fig. 18. *Str. gran.* stratum granulosum; *int. theca,* internal theca; *ext. theca,* external theca, in which are seen the fibres. *s.m.f.*, which have been identified as smooth muscle fibres. *Mem. lim. ext.* membrana limitans externa, in this specimen not very clearly defined. ×600. Specimen O 2. 80.

also obtained from other specimens stained by Mallory's method, wherein corresponding groups of fibres were stained distinctly purple in contrast with the surrounding bright blue colour; whilst in other sections of different follicles subjected to the influence of Congo red, the same tissue elements were revealed stained a dull violet, contrasted with the grayer colour of the tissue around. It is only fair to say that these results were not obtained in all the specimens examined, but so convinced was I of their significance that I em-

ployed other and more refined methods, with confirmatory results. Fearing lest my observations might be biassed, I handed over some unstained sections to my friend Mr H. M. Carleton, the Demonstrator in Histology, with the request that he would subject them to a careful examination. This he took great pains to do, and finally admitted that on histological grounds, no less than by reason of the staining reaction, the tissue undoubtedly contained smooth muscle fibre. From my own material I am enabled to furnish a figure of a highly magnified microphotograph which demonstrates these features (fig. 19).

Whilst there is thus undoubted evidence of the presence of smooth muscle in the external theca of the follicle, it is interesting to note that with certain reagents, we may obtain, under a low power, a general view of the distribution of this muscular element throughout the substance of the ovary as seen in section. This is best demonstrated in sections stained with safranin and light green; the colour differentiation effected is such as to indicate the presence of a tissue of a peculiar staining quality which invades the substance of the ovary along the line of the great vessels and follows them outwards as they reach the area of their distribution towards the cortex. The general arrangement of this particularly coloured zone conforms closely to the distribution of the blood vessels as indicated in the figure which Clark (6) has published in his account of the blood vessels of the ovary. As may there be seen, the smaller vessels are traced to the walls of the follicle, accompanied no doubt by the strands of smooth muscle, whose general course is indicated by their greater affinity for one of the constituents of the double stain. In the specimen examined the contrast between the differently stained areas was sufficiently pronounced to indicate the general distribution of the smooth muscle.

In the human ovary it thus appears that smooth muscle is present in considerable quantity, not so abundant as may be seen in lower forms, but still in such amount as to play a considerable part in the functioning of the organ.

According to Winiwarter ((36), p. 639), all attempts have hitherto failed to demonstrate the presence of this muscular element by experimental means. I therefore consulted my friend Dr Gunn, the Professor of Pharmacology here, who, after having had his interest enlisted in the question, determined to make a fresh attempt. He reports as follows: "The ovary (a rabbit's) was suspended in a bath of oxygenated Locke's solution at body temperature. Movements were recorded by a light-lever of high magnification, the method used being the same as has been widely employed for the isolated uterus and other organs. No spontaneous movements were shewn by the ovary. In one experiment the ovary of a full-grown virgin rabbit shewed on the addition of adrenaline to the Locke's solution (in concentration of 1 in 200,000) a contraction of the ovary characteristic of smooth muscle. Adrenaline stimulates the sympathetic nerve ends in smooth muscle. The sympathetic nerve is a motor nerve to the rabbit's uterus. The experiment therefore indicated that the ovary contains smooth muscle, innervated by the sympathetic, and that the innervation of

the ovary is qualitatively the same as of the uterus (in the rabbit). With high lever magnification the amplitude of excursion was very small, indicating a very small amount of contractile tissue."

This experiment seems to set at rest all doubts as to the presence of functionally active muscular fibres within the stroma of the ovary, and as we have already seen that fibres answering to the histological details of smooth muscular fibres and reacting similarly to selective stains occur within the wall around the Graafian follicle, it is evident that we have to hand a means which may play a not unimportant part in the rupture of the follicle.

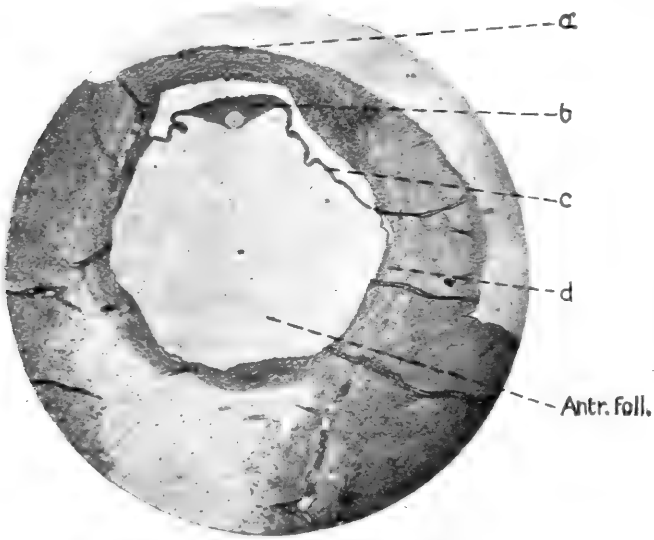

Fig. 20. Section through a nearly ripe human Graafian follicle; *a*, the surface of the ovary; here the follicular wall is only about ·2 mm. thick; *b*, the cumulus containing the mature ovum, note that it lies on the superficial aspect of the follicle, immediately opposite and close to the thinnest part of the follicular wall. Both the cumulus (*b*) and the stratum granulosum (*c*) are separated from the internal theca in the upper hemisphere; *d*, the external and internal thecae combined, the magnification is not sufficiently high to differentiate these layers. In the lower hemisphere of the follicle the cells composing the stratum granulosum are still adherent to the inner surface of the follicular wall, the membrana limitans externa alone intervening; the magnification is not sufficient to shew this layer; *antr. foll.* antrum folliculi. × 18. Specimen 453 A. 35. 4.

The Rupture of the Follicle

Having passed in review the various structures which enter into the formation of the Graafian follicle and its contents, it may now be possible to discuss the means by which the follicle ultimately ruptures and sheds its contents. Before, however, proceeding to consider this question, it may not be without advantage to reproduce a microphotograph of a Graafian follicle which must have nearly reached the stage at which its rupture was imminent, to judge by the appearances displayed (fig. 20).

The estimated size of the follicle is 2·00 × 1·96 × 1·63 mm. As is readily seen, the superficial wall of the follicle, i.e. that separating its cavity from the surface of the ovary, is thin, only 0·2 mm. thick. The ovum contained within the follicle is judged to be mature, since there is present in it a divided first polar body, together with a second polar body, whilst the nucleus appears to have returned to the resting condition. A figure of this oöcyte has already been published in my previous paper on the maturation of the ovum (33). For all these reasons, we are justified in supposing that the follicle is ripe, and has reached the stage in its existence when its collapse, and the liberation of its contents, cannot for long be delayed if the physiological necessity arises.

But an examination of the figure enables us to realise certain unusual features. First, we recognise that the ovum, surrounded by the cumulus, is so disposed that it lies superficially within the follicle, and near, and in immediate correspondence with the line of the stigma—the site corresponding to the point of rupture. But secondly, it is obvious that throughout the superficial hemisphere (i.e. that directed to the surface of the ovary) the stratum granulosum with the cumulus has become detached from the inner surface of the internal theca; elsewhere, over the inner surface of the posterior hemisphere, it still remains attached.

Obviously no better arrangement could be devised for the expulsion of the ovum than that shewn here, for if the rupture be due to an increase in internal pressure, the ovum would naturally, by the bursting pressure, be forced through the orifice made in the weakened wall when that gave way. Unfortunately, as we have already seen, the position of the ovum and the cumulus is not always superficial, but may be, and often is, situated in relation to the deep surface of the follicle, at a point opposite and farthest removed from the stigma, in which case it is difficult to understand how, when the rupture occurs, the discharge of the ovum is effected. Under these circumstances the doubt arises in one's mind, as to whether the ovum is not more likely to remain lodged in the bottom of the empty cup.

The detachment of the cells of the stratum granulosum from the inner surface of the internal theca is a matter which has already attracted a considerable amount of attention. The prevailing opinion is that the condition is to be regarded as an artefact—that it is due to the retraction induced by the coagulation of the liquor folliculi. Such an explanation seems feasible, and is possibly the one that comes readiest to hand; before accepting it, however, there are some other considerations that must be taken into account.

In the numerous examples of this condition which I have studied, I have been struck with the fact that there is not always such a correspondence in the contours and area of the retracted surfaces of the stratum granulosum and the internal theca as one might expect if the separation of the layers were effected by such mechanical means. It is not uncommon to find the stratum granulosum floated well into the centre of the follicle, and twisted and infolded in such a way as to suggest that these layers were afloat in the fluid

contained within the follicle at a time prior to its coagulation. Further, they often exhibit appearances as if undergoing disintegration, and are frequently fragmented. In dealing with human material it is only fair to say that putrefactive processes must not be overlooked. Yet withal, I confess I am by no means assured that the condition is thus easily explained as being due to the effects of coagulation by fixation.

There are additional reasons for hesitating to accept this view. First, the case in which the cumulus is so disposed as to lie on the deep surface of the interior of the follicle, the site assigned to it by Nagel and others as normal. Under those circumstances it is difficult to see, as has just been observed, how by any pressure sufficient to burst the follicle the ovum could be expelled through an opening opposite in direction to the force to which it was being subjected. As has been said, a more reasonable supposition would be that it would be left in the bottom of the cup, and this, be it observed, is what is supposed to have happened in those cases of ovarian pregnancy which have been recorded, the explanation offered being that the ovum has failed to escape from the ruptured follicle and that the entering spermatozoön has fertilised it *in situ*.

Second. Thanks to the kindness of Professor Robinson, I have had an opportunity of seeing, amongst his collection of ferret material, an ovum, just within the oviduct, apparently recently discharged from its follicle, which, besides being surrounded by the cells of the cumulus, had, attached to these, tags of tissue which could only be accounted for on the supposition that they were remains of the sheet of the surrounding stratum granulosum.

Third. In one case I had the opportunity of examining a human Graafian follicle which must have been quite recently ruptured. In this I failed to find any trace of follicular cells—all that remained was the enfolded and engorged internal theca, very definitely lined internally by the membrana limitans externa, without any trace, so far as I could see, of any follicular cells overlying it. Within what was left of the cavity of the follicle were a few scattered blood cells only[1].

This raises of course the vexed question of the origin of the corpus luteum. Von Baer in 1827 propounded the view that the corpus luteum was derived from the theca interna. This conception has been supported by Valentine, His, Rokitansky, Kölliker, Gegenbaur, Paladino, Nagel, Bonnet, Schottländer, Minot, Williams, Clark and others.

On the other hand Bischoff in 1842 expressed the opinion that the corpus luteum is derived from the follicular epithelium. This view has received support from Meckel, Pflüger, Luschka, Waldeyer, Sobotta, Honoré, Marshall, Van der Stricht, Heape, and Kries, amongst others.

Rabl in 1898 suggested a compromise, and concluded that the lutein cells

[1] It is interesting to note that this specimen was obtained from the ovary of a woman whose uterus exhibited evidence of the onset of menstruation.

have a double origin, arising both from the membrana granulosa and from the theca interna[1].

Into this controversy I am not at present prepared to enter; all I can say is that the human specimen I have here mentioned appears to confirm in every respect the original contention of Von Baer.

There can be little doubt but that the liquor folliculi serves two useful purposes: it acts as a source of nutrition for the ovum, as well as providing a means for its protection. The production of this fluid by the disintegration of the follicular cells through the agency of the so-called bodies of Call and Exner has been already discussed (see p. 14), and need not now be further alluded to. During this process of the dissipation of the follicular cells, with a concomitant increase in the size of the antrum folliculi, there also appears to be taking place a reproduction of these follicular cells to replace the wastage, as evidenced by the occurrence of mitotic division observed amongst them. To what extent this takes place it is difficult to say, but apparently there comes a time when this source of reinforcement is reduced to the thin single layer of cubical cells which represents all that is left of the stratum granulosum. In some instances, the conditions are such that this remaining layer may all but disappear, in fact in some cases I have failed to find evidence of it in parts of the circumference of the follicle.

Support is given to this view by the observations of Miss Lane-Claypon ((16), p. 42) on the ripe Graafian follicle of the rabbit, in which she describes "almost complete disintegration of the membrana granulosa."

A fact of some interest, be it noted, is that this condition is not necessarily met with in follicles which one would regard as fast approaching their rupture, as judged by their very superficial position and the thinness of their overlying wall. This activity on the part of the follicular cells is no doubt sustained by the nutrition derived from the fluids of the blood through the agency of the capillaries of the internal theca, and possibly the liquor folliculi itself may be increased in bulk by an admixture of constituents derived from both sources.

In this connexion, it is well to remember that interposed between the peripherally placed follicular cells and the capillary zone of the internal theca, there is the membrane which has been already alluded to as the membrana limitans externa (basal membrane). Now, as stated, there is considerable doubt as to the constitution of this membrane. We have seen that the union between this membrane and the follicular cells is generally speaking very feeble, and that the follicular cells are extremely liable to be detached therefrom, it may be by artificial means, or possibly as the result of a normal process. In the accompanying figure (fig. 21) there seems strong evidence for believing that the separation of the stratum granulosum and the internal theca is effected by the infusion of fluid between the two layers of the membrana externa, and not by the dragging away by retraction of the membrana externa from

[1] For the literature of this subject I am indebted to the papers of J. G. Clark (5) and F. H. Marshall (19).

the internal theca, else how can we account for the appearance of distensions within these spaces and the concavity of their walls?

As a consequence of this separation, whilst in the majority of cases the bulk of the membrana limitans externa adheres to the inner surface of the internal theca, yet the evidence produced (see fig. 15) of the splitting of this layer so that one lamina adheres to the follicular cells, whilst the other remains in contact with the internal theca, suggests that the structure of this layer is not so homogeneous as is usually described, but that sandwiched between its

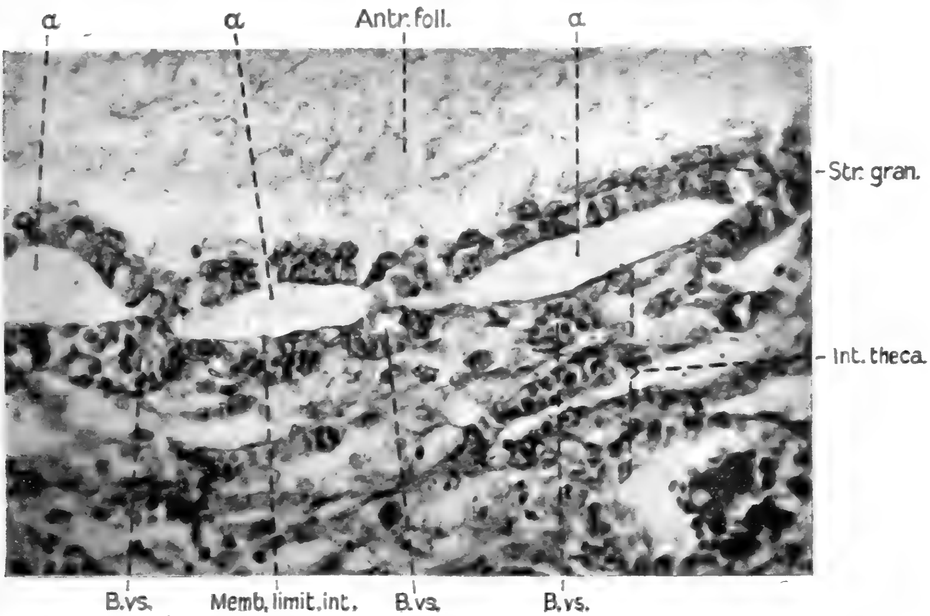

Fig. 21. Section of human follicular wall shewing the commencement of the separation of the stratum granulosum (*str. gran.*) from the internal theca (*int. theca*). This appears to involve the splitting of the membrana limitans externa through the distension of the lymph spaces in it, so that larger spaces (*a, a, a*) are produced, the walls of which through their concave contours afford evidence of a pressure from within, due to the accumulation of fluid inside the spaces. Note the position of the capillaries (*B.vs.*) of the internal theca (*int. theca*) in relation to these spaces (*a, a, a*) the walls of which are formed by the split membrana limitans externa, one layer of which adheres to the internal theca, the other forming what looks like a basement membrane to the external layer of cells of the stratum granulosum. *Antr. foll.* antrum folliculi filled with a reticulated coagulum. ×400. Specimen 453 B. 30. 6.

inner and outer strata there may be a weaker element, or, what is more probable, a series of lymph spaces in direct contact with the capillaries of the internal theca, as seen in the figure, on the one hand, and the bedded bases of the follicular cells on the other.

This splitting of the external limiting membrane is a feature to which Robinson ((27), p. 320, plate X, figs. 58 and 67) has already called attention, though he attributes it to the use of fixatives. Granted that it is so, it may be

the means of revealing potential spaces which at the time may not be distended, but this in no wise precludes the possibility of these being tissue fluid channels.

My reason for dwelling on these facts is that they may possibly afford an explanation of what happens when the follicle bursts. Various opinions have been expressed in regard to the mechanism which brings about this phenomenon. The generally accepted view is that by a gradual increase in the bulk of the contents of the follicle such a pressure is induced as will lead to the rupture of the gradually weakening wall in the region of the stigma.

On the other hand, some, in order to bring the details more into accord with the accepted facts, suggest that the rupture of the follicle is induced by a sudden increase in the follicular pressure.

Nagel ((23), p. 60) and his followers attribute the rupture to changes taking place in the tunica interna, whereby its vessels become highly developed, and its cells multiply enormously, every cell increasing in size by the growth of its protoplasm, at the same time the protoplasm becomes filled with a peculiar crumbling mass of which nothing more definite is known, from which the whole inner wall of the follicle (in the fresh condition even before its rupture) acquires a yellowish colour. The tunica interna thus altered has an undulating appearance, while its cells, which are now called lutein cells, and form a strong layer many rows thick, are arranged in the form of papillae, into every papilla runs a much-branched vessel. Through this growth of the lutein cells the contents of the follicle are pushed towards the thinnest part of the follicle (stigma) on the surface of the ovary, and thus the follicle is brought to its rupture.

In respect of this I can only say that my own observations have not enabled me to recognise these conditions in the still unruptured, though apparently ripe follicle. The appearances described are such as are readily recognised in the freshly ruptured follicle, preliminary to the formation of a corpus luteum, though here unfortunately we are unable to form other than an approximate estimate of the time which may have elapsed between the rupture and the examination of the specimen.

Clark (6), in discussing the matter, in part attributes the dehiscence of the follicle to the peculiar arrangement of the vessels of the ovary, and was able to demonstrate the rupture of the follicle following the introduction of a carmine-gelatine injection. He also considers the occurrence of haemorrhage within the follicle more frequent than its absence.

Heape (13) considers that in the rabbit the rupture is induced by the stimulation of the erectile tissue, and not simply as a result of internal pressure arising from increased vascularity, or a greater amount of liquor folliculi.

In a series of experiments Schochet ((30), p. 241) indicates that the liquor folliculi possesses a digestive enzyme that can be demonstrated by dialysis and other tests. As a tentative interpretation it is suggested that the rupture of a Graafian follicle is due in part to the digestion of the theca by the liquor folliculi.

Winiwarter ((36), pp. 640–41), in discussing the function of the smooth muscle met with in the ovary, reviews the suggestions previously made by Rouget (28), and Aeby (1), that the muscular tissue plays its part "by setting in action a complex mechanism subject to physiological conditions of which we are ignorant, and which simple galvanic stimulation cannot reproduce," the conclusion being that "the ovary, together with all the internal genital tract, can undergo erection under the influence of a stimulus aroused, in the ovary, by the distension of the Graafian follicles; the increase of tension in the ovarian stroma brings on the rupture of the follicle, after which relaxation follows; it is therefore the muscular tissue of the mesovarium which plays the active part." This hypothesis is also supported by Grohe (11).

Winiwarter's own conclusion is that the muscular tissue in the mesovarium acts in part by controlling the venous return from the organ, thereby conferring on it an erectile power, probably associated with the period of rut, or, it may be, aroused by the stimulus of coitus, whilst he suggests that the presence of smooth muscle in the external theca of the Graafian follicle may be a determining cause of its rupture.

Furthermore, it has frequently been suggested that the congestions which occur within the pelvic organs at the menstrual periods, and the turgescence of the associated organs which may occur during coitus, may have something to do with the rupture of the follicles.

It is too complex a problem here to discuss the question of the relation of ovulation to menstruation, suffice it to say that the bulk of the evidence seems to point to the fact that there is an intimate association between the two phenomena, and that consequently those vascular changes which we associate with the one may be in part responsible for certain of the processes connected with the other.

As Eden puts it ((7), p. 6): "It is undoubtedly true that ovulation and menstruation are closely related to one another. Whether they are coincident or consecutive, and if consecutive, which precedes the other, we do not know with certainty."

Barnes ((2), p. 455), Dr Clelia Mosher (21) and Helen MacMurchy ((17), p. 909) quoting Giles ((10), p. 115) and Dr Mary Jacobi (15), are all agreed that there is normally a rise in blood pressure for a day or two prior to menstruation, and a fall immediately on the onset of the flow.

I am aware that the occurrence of apparently ripe Graafian follicles has been recorded in young children prior to menstruation, and even in some instances in the new-born child (Nagel (22), p. 413), but there is no evidence that these ever ruptured or that the ova therein contained were capable of fertilisation; it is much more probable that the follicles became atretic.

Considering the foregoing suggestions and the observations on which they are based, it would appear that well-nigh everything that could be said on the subject had been already stated. A little reflection, however will, I hope, induce the reader to believe that there are other ways of interpreting the

phenomena, and so bringing them more in line with what experience would support.

I have endeavoured to suggest that the main function of the liquor folliculi is to nourish, conserve, and protect the delicate ovum as it lies within the follicle. Evidently a time arrives when, from the appearance presented, the further production of the liquor folliculi by the disintegration of the follicular cells is arrested, as evidenced by the reduction in number and change in character of the residual follicular cells. At this stage we may assume that the pressure within the follicle is stabilised, and may remain for unknown periods undisturbed. It is therefore hard to believe that the pressure within the follicle can be rapidly raised by any sudden increase in the amount of the fluid derived from the follicular cells.

We have around the follicular cyst, if such I may call the liquor folliculi enveloped by the stratum granulosum, a capillary plexus subject to all the controlling influences of the sympathetic nervous system.

We have already alluded to this capillary zone as essential to the nutrition of the follicular epithelium, though to what extent the liquid constituents of the blood may contribute to the fluid bulk of the liquor folliculi we have no information; but assuming that the liquor folliculi is in main the product of the follicular cells, it by no means follows that, since the source of that supply is no longer active, the fluid derived from the blood in the capillaries contributes no further to the increase in fluid contents of the follicular cyst; controlled as is this supply by the sympathetic, it must necessarily react to such stimuli as induce changes in the circulation directly concerned, or, it may be, in harmony with vascular changes induced in the tissue around.

Sexual thoughts, sexual desires, coitus, the congestion associated with menstruation, may all play a part, with what result?—the immediate and sudden increase in pressure, involving, it may be, the transudation of a greater quantity of the fluids of the blood, and thus increasing the pressure contents of the follicle to its straining point. I suggest that in this process, when dealing with a follicle the contents of which are ripe for discharge but quiescent, the effusion of fluid poured out from the capillaries invades those lymph channels which, we have reason to believe, intervene between the cells of the stratum granulosum and the internal theca, thereby tending to separate the granular layer from the inner wall of the follicle, and thus leading to the release of the cumulus and its anchoring layers, so that it, with the contained ovum, lies free and floating within the cavity of the follicle in such a way that it must follow the stream of the fluid on its expulsion and release through the rupture.

In this way, possibly, is effected the liberation of the ovum and its associated follicular cells from the wall of the follicle, which Böhm and Davidoff (3) have suggested as an initial stage in the escape of the ovum from the ruptured follicle. According to these authors the ovum and the cells of the surrounding cumulus, or discus proligerus, ultimately come to lie free and floating within the liquor folliculi, a process which in their opinion is effected by the softening

of the cells of the pedicle of the cumulus, which thus leads to the separation of the cumulus and the contained ovum from the stratum granulosum. I do not deny the possibility of this happening, but I have not so seen it in any of the specimens I have examined, for in all the cases in which I have been able to follow, through a number of serial sections, the relations of an apparently free cumulus as displayed in some sections, on careful search I have been able invariably to trace its connexion with the stratum granulosum in other sections. For these reasons I suggest that the same end is accomplished by the stripping off of the entire follicular cyst from the inner wall of the internal theca by the rapid effusion of fluid derived from the capillaries, for in no other way can we account for the somewhat sudden increase in pressure which appears to be a necessary accompaniment of the process of ovulation.

Whilst admitting that this is a phenomenon which is dependent on effects primarily induced by the nervous mechanism controlling the circulation, we must not overlook the fact that there are other contributory causes that may play a part. We have hitherto assumed that the increase in internal pressure, effected as suggested, is the determining cause of the rupture of the follicle, for as soon as that pressure exceeds the resistance of the weakened wall of the follicle in the region of the macula or stigma, rupture must inevitably take place. On the other hand no regard has been paid to the possible influence of muscular contraction as the determining cause of the rupture of the follicle. The occurrence of smooth muscle fibre within the stroma of the ovary and mesovarium is generally admitted. Why is it there? Of what use may it be? Winiwarter ((35), p. 640) has already suggested that, by its contraction, the return of the flow of blood through the veins may be retarded, thus leading to a state of engorgement or erection of the organ, which will of course react on the capillary circulation and thus promote a more vigorous transfusion of the fluid constituents of the blood, thereby increasing the amount of lymph at certain selected and appropriate points; in this way, doubtless, assisting in increasing the bulk of the follicular contents. At the same time that author foreshadows the possibility of this smooth muscle acting as a potent factor in the rupture of the follicle, for he describes the disposition of this muscular tissue as not merely scattered throughout the stroma of the ovary, but also forming a definite layer in the external theca of the follicle.

After the demonstration which I have here given of the occurrence of a definite muscular layer in the wall of the human Graafian follicle (see figs. 18 and 19), it would seem that we are justified in assuming that this definite concentric layer fulfils some useful purpose. Its arrangement and disposition inevitably suggest that by its contraction a compressing effect, rapid and immediate, will be exercised on the contents of the follicle, thereby increasing the internal pressure and consequently determining the rupture of the follicle.

How are these facts in accord with the results of experience? Assuming that in the human female in the virgin condition there is a periodicity in ovulation coincident with that of menstruation, we have an explanation of

this apparent association, because, at that period, we have reason to believe that the ovary shares in the general engorgement which occurs throughout the genital tract; under these circumstances the conditions are such as to lead to a slow and gradual increase in the amount of the fluid contents of the follicle as derived from the blood, and distinct from those which are the product of the follicular cells, which, be it noted, in a follicle fast approaching maturity, have no further reserve to call upon. The further increase in the fluid contents of the follicle is therefore dependent on conditions determined by the local circulation, and if this condition be steadily maintained, there is little difficulty in realising how the pressure may ultimately overcome the resistance, and so the rupture of the follicle may be effected without any necessary sexual disturbance other than that involved in the psychic and emotional changes induced by menstruation.

On the other hand, there is reason to believe that ovulation takes place at other times, and in other ways, than what may be termed the routine method. It is a matter beyond dispute that under the influence of intense sexual excitement, in coitu, women are occasionally cognisant of strange happenings, which they fail to describe, but by which they are deeply impressed. Is it unreasonable to suggest that these sudden, ill-defined and deep-seated sensations are the result of the rupture of a Graafian follicle? The facts seem to fit the case. Granted the presence of an all but ripe and superficially disposed Graafian follicle in what we may term a quiescent condition; if the action of the mechanism above suggested be accepted, we have all the means necessary to bring about rapid rupture. The exalted state of the circulation will assist in the rapid accumulation of fluid within the follicle, and its subsequent distension, whilst the instant response of the muscular element in the wall of the follicle to the call of the sympathetic will immediately result in a combination sufficiently effective to ensure the rupture of the follicle and the discharge of the ovum.

If, under these conditions, this explanation be accepted, it would seem to indicate that possibly the same may occur associated with minor degrees of sexual excitement, so that, whilst in the human female ovulation may, in the ordinary way, coincide with and be associated with the vascular changes concomitant with menstruation, yet there may be no bar to the rupture of a Graafian follicle at any other time, provided such be ripe, in the sense that the ovum is mature, that the follicular cells have discharged their function by providing the necessary nutriment and affording the requisite protection, and assuming always that the follicle has acquired such a superficial position in the ovary as will permit of its rupture. There is reason to suspect that it may remain quiescent in this position until such conditions arise as may lead to increased vascular activity, or it may be the incidence of such stimuli as may react on the smooth muscle involved and so accelerate the process.

If it be doubted that the involuntary muscular fibre in the wall of the follicle can act in this way, I would urge that we have abundant evidence

of its power of contraction in the appearance displayed in the wall of the follicle after rupture, for there seems little doubt that the infolded appearance of the engorged internal theca is in major part due to the compression exercised by this contracting element, for there is no evidence of the presence of elastic tissue to bring about this result.

RÉSUMÉ

Briefly summarised the conclusions arrived at are as follows:

1. There is reason to believe that the size of the ripe human Graafian follicle is usually very much overstated in the text-books. In the author's experience it is doubtful if Graafian follicles over 5 mm. in diameter are normal.

2. The position of the cumulus is *not*, as frequently stated, always situated in the deeper part of the follicle, i.e. that furthest from the surface of the ovary. It may occur in any position, but in the material available appears to occupy a superficial position in about 50 per cent. of cases.

3. The so-called bodies of Call and Exner are follicular cells or groups of cells undergoing such changes as result in their ultimate liquefaction and disappearance to form the liquor folliculi.

4. The radial arrangement of the follicular cells around these bodies is a purely mechanical result and is in no wise concerned with the elaboration of the material which they surround.

5. The resulting liquor folliculi, primarily derived, as explained, from the follicular cells, is destined for the nutrition, conservation and protection of the ovum. It is doubtful whether it plays any active part in the subsequent rupture of the follicle, the necessary increase in the tension of the follicle being provided at the appropriate time by transudation of fluid from the blood circulating in the internal theca of the follicle.

6. The stratum granulosum may be reduced to a single layer of cubical cells. In some instances there is reason to believe that even this layer disappears.

7. In consequence of this reduction in the number of follicular cells, there comes a time when no further liquor folliculi of follicular origin is produced. When this stage is reached, there is reason to believe that the follicle may remain quiescent till other influences are brought into operation to determine its rupture.

8. The cells of the stratum granulosum rest upon the membrana limitans externa, a delicate layer which separates these cells from the inner surface of the theca interna.

9. It is noteworthy that the cells of the stratum granulosum strip off very readily from the membrana limitans externa. There is reason for suspecting that this under certain conditions is a normal process resulting in the liberation of the ovum so that it floats free in the liquor folliculi.

10. There is evidence for believing that the membrana limitans externa is not a simple single layer, but is permeated by potential lymph spaces, which on being distended lead to its splitting into two layers.

11. On this assumption the cells of the stratum granulosum are therefore separated from the capillaries of the internal theca by a network of lymph channels into which the fluids of the blood may under certain conditions be speedily discharged.

12. The rapid exudation of fluid in this situation has two consequences: it strips the cells of the stratum granulosum off the inner wall of the follicle and thus liberates the ovum and cumulus, and at the same time rapidly increases the pressure within the follicle.

13. It is noteworthy that the vascularity of the internal theca increases as the age of the follicle advances, that it tends to be more pronounced in that part of the internal theca corresponding to the site of the cumulus, and in the later stages least in the position overlying the stigma.

14. The amount of blood circulating in this capillary plexus will be determined by the conditions which control the surrounding circulation, either by increasing the flow, or, it may be, by retarding the venous return, the latter, as suggested by Winiwarter, being possibly due to the action of the smooth muscle constricting the veins and so leading to a turgescence of the tissue.

15. Such vascular conditions may be associated with the congestion and increased arterial pressure which precedes the appearance of the menstrual flux, or may be the direct result of some excitatory stimulus of a sexual kind operating through the sympathetic.

16. In either case the immediate result may be increased transudation of tissue fluid into the follicle with the results stated in paragraph 2.

17. It is probable that under what we may regard as the normal condition of ovulation in the sexually inactive female, the vascular disturbance associated with menstruation is alone sufficient to raise the intrafollicular pressure to the bursting point.

18. In the sexually active female there is reason to suppose that the same effect may be independently induced by stimuli which react through the sympathetic nervous system, provided there is at the time a quiescent ripe follicle present in the ovary.

19. In such cases no doubt the muscular element in the ovary plays an important part, more particularly that part of it which occurs in the external theca of the follicle, for this, by contracting on a follicle already undergoing distension owing to the exalted condition of the vascular supply, will naturally tend to increase the intrafollicular pressure and so lead to the rupture of the follicle.

20. If these conclusions be true it would follow that ovulation is not necessarily limited to one particular period, but that under the influence of appropriate stimuli it may occasionally occur at other times as well.

In conclusion, I must express my thanks to my Laboratory Assistant, Mr W. Chesterman, and to Miss Beatrice Blackwood, for the assistance which has enabled me to carry out this research; they have both been untiring in their efforts to carry out my every wish, and I am deeply sensible of their help and co-operation.

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VOLUNTARY MUSCULAR MOVEMENTS IN CASES OF NERVE LESIONS

By Prof. FREDERIC WOOD JONES, D.Sc.

When, after the experience of a few months of war, peripheral nerve lesions came to be treated upon what may be termed a wholesale scale, it was felt by many clinicians that their experiences were fast outrunning the amount of exact anatomical information obtainable in most of our text-books. In no connection was this state of affairs made more manifest than in dealing with those cases which demanded a precise knowledge of the action of living muscles in the human body. Our anatomical text-books gave the actions of the muscles, they also gave the innervation of these muscles, and the lines along which information for the clinicians was to be had, consisted in arguing that since a particular nerve has been divided, certain muscles will be paralysed, and therefore the actions carried out by these muscles will not be performed. The first stumbling-block—the lack of precise knowledge as to the arrangement of the motor fibres in mixed nerves, and the exact site of origin of branches to individual muscles—was soon largely rectified, but the question as to what action any living muscle can actually perform is, as it always has been, a difficult one to settle. Now, it has been within the experience of everyone who has come in contact with a large series of cases of nerve lesions that, at times, after the undoubted division of a motor nerve, the resultant paralysis has not been so great as would have been expected from a study of text-book anatomy. If it is taught in the text-books that a certain joint is bent by the action of a definite muscle, and this muscle is supplied by a definite nerve; then, when this nerve is divided, the expectation will be that since the muscle is paralysed, the action of bending the joint will not be performed. Not by any means uncommonly, this expectation is not fulfilled, for the patient continues to possess the power of bending the joint. Two explanations are at once forthcoming to account for this anomalous state of affairs. It is possible that, in this particular case, the nerve supply of the muscle is not that which is usually given in the text-books—that some other nerve sends branches to the muscle, and it is not paralysed at all. Or, it is possible that it is paralysed, and that some other muscle, or combination of muscles, may perform the action usually regarded as the exclusive function of this one. The first alternative has had its advocates, but we, as anatomists, need have little fear that a large revision of the text-book teaching upon the nerve supply of muscles will be necessary as an outcome of the study of war injuries. As a matter of fact, routine electrical testing upon the structures as they are exposed on

the operating table, should form a part of all operative work, and when this is carried out, the instances in which an appeal has to be made to abnormality of nerve supply, are reduced to a minimum. In all cases cited in this paper this procedure has been adopted. With regard to the second alternative, there is still a great deal of confusion. Much erroneous teaching has been put forward during the war, and many false conclusions arrived at in consequence of the deceptive nature of some of the voluntary movements possible after complete section of motor nerves. Testing voluntary movements is a business to be undertaken with a judicial mind, and at the best it is a difficult affair. It is easy to determine that a joint bends: it is by no means easy to determine beyond doubt what agent caused its bending.

It must never be forgotten that in testing voluntary movements, we ask the patient to perform some action;—we do not ask him to use certain muscles. The cortex of the patient neither knows nor cares of muscles, and his volition will therefore be effected by any agent capable—even in the lamest, and most halting way—of carrying out the volition. In some cases no agent having the power to perform the desired movement will be at hand, but at times some muscle may achieve a flicker in the right direction, or at times a perfect substitute for the paralysed muscle is prepared to take on the work. In any case, whatever beginning can be made at the business of reproducing the lost movement, it is probable that it will be steadily cultivated by the patient. The effort to perform a cortical volition by *any* agent is very remarkable, the most unlikely muscles will contract in an endeavour to effect the desired movement;—no man can flex his wrist with his platysma, but if the medical officer and the patient are both determined on doing their best, many men will attempt it. Among the muscles which will be called on in the attempt to perform a lost movement, are the antagonists of the desired movement, or any or every member of the groups of muscles having a general antagonism to the movement of volition. If, as a substitute for the paralysed flexors of a joint, the extensors of that joint be cortically activated, the volition of flexing will naturally not be attained; but if the extensors of some neighbouring joint be contracted, it is possible that a relative and passive flexion of the paralysed joint will result, and thus the volition may be achieved. Once the patient has learned this trick, the chances are that he will cultivate it, and the working of his perfected effort may be extremely difficult to detect. In the limits of the present paper, I have included "trick" movements, because although they do not throw much light upon normal muscular movements, they have led some observers to false assertions as to the incorrectness of orthodox text-book teaching.

In all the cases which are recorded here, and from which conclusions are drawn, the author has personally seen the condition of the nerve as exposed at the operation, and has checked the finding by the electrical tests. If a nerve is reported as divided, the statement means that the author has seen the complete severance in the continuity of the nerve, and witnessed the failure

of the exposed nerve to react to faradic stimulation. When movement is spoken of as being produced by the action of muscles, it must be understood that a real active movement of the part is achieved. In no case has a mere questionable flicker been reported as a voluntary movement. In all cases illustrated, the patient has been so arranged that the active movement has been carried out against the action of gravity.

A. *Complete division of the musculo-cutaneous nerve*

Paralysis of biceps and brachialis anticus. This is not at all a common lesion, and in only one of the cases that I have seen was the nerve actually

Fig. 1. Paralysis of biceps and brachialis anticus. Plexus lesion. Driver S.
Flexion of elbow produced by supinator longus.

severed by the passage of a projectile. In only one case of complete division (Pte. G. H. 8th R. Sussex, 2288), with the musculo-spiral intact, was there any evidence that the brachialis anticus retained any power of contraction. In this case the contraction was palpable but localised, and even in the most advantageous position it failed to produce any flexion of the elbow. In every case of paralysis of the biceps and brachialis anticus in which the musculo-spiral nerve was intact, the elbow was capable of immediate and strong flexion produced by the supinator longus (see fig. 1). Despite recent teaching, the supinator longus is always a flexor of the elbow joint. The

flexion of the elbow produced by the supinator longus is a powerful and precise action, and it is carried out with the hand in a useful working position. It is indeed often a matter of great difficulty to re-educate the patient in the use of the brachialis anticus and biceps, even after these muscles have perfectly recovered their voluntary contractibility.

B. *Complete division of the musculo-cutaneous and the musculo-spiral nerves*

Flexion of the elbow is performed by the pronator radii teres (see fig. 2). This flexion is nothing like so powerful, nor so complete, as that produced by

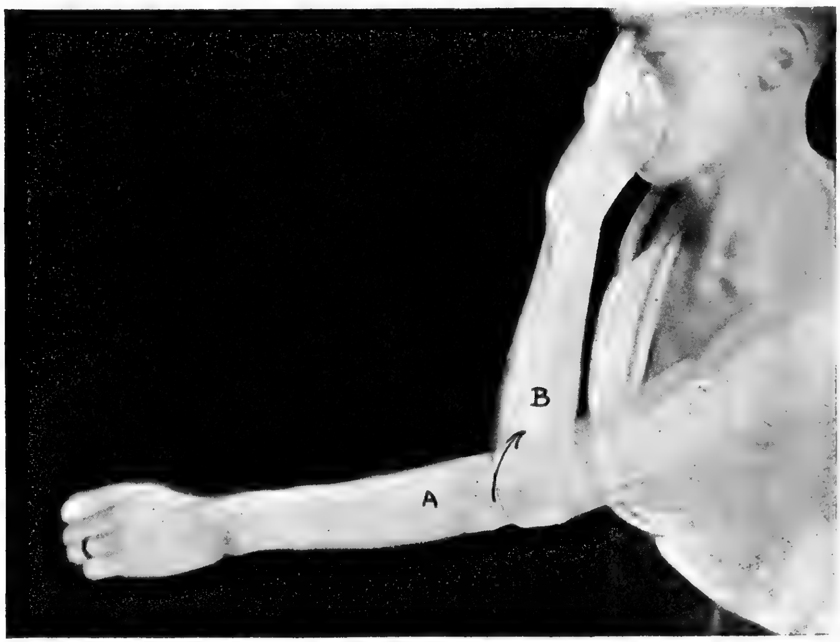

Fig. 2. Complete division of musculo-spiral and musculo-cutaneous. Lieut. L. B., gun-shot wound, left axilla, 24. iii. 18. Both nerves found divided, 22. iii. 19. *Flexion of the elbow produced by the pronator radii teres.*

the supinator longus. The action requires some cultivation by the patient, and even after a considerable interval the flexion may not be sufficiently complete to raise the hand to the mouth. In the case illustrated, the pronator radii teres was the only muscle which was used to perform the action, and the flexion produced was a forcible and useful movement when the forearm was maintained fully pronated.

The action of the biceps upon the elbow joint. Since there has recently been some attempt at revision of the established teaching concerning the action of the biceps as a flexor of the elbow joint; it is worth recording that apart altogether from the phylogenetic history of this flexor, and its undoubted

action as a flexor in the normal living human subject, its action is well seen in a very wide series of war injuries. Contracture of the elbow joint following a flesh wound limited to the biceps muscle is a common enough condition, and is comparable with the flexion of the knee so commonly seen following flesh wounds of the hamstrings. Cases of spasm of the biceps may follow prolonged splintage or slinging, and may be maintained with a hysterical basis for a period extending over years. (Case. Pens. G. C. 6 Glocs. 267306, shrapnel flesh wound middle R. Biceps—elbow flexed to right angle from 19. 7. 16 to 19. 5. 19. No other muscle or nerve involved.) Discrete contracture of the biceps fascia, without the involvement of any other structure, also produces flexion of the elbow.

C. *Complete division of the musculo-spiral nerve*

(1) Paralysis of the extensors of the wrist. Although "drop wrist" is such a classical symptom of musculo-spiral paralysis, and although it is so strikingly

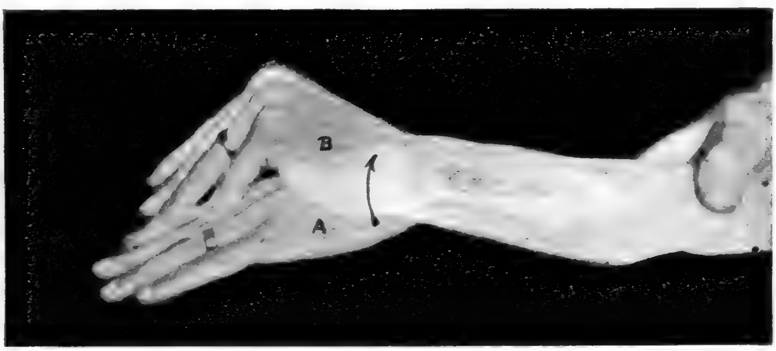

Fig. 3. Complete division of the musculo-spiral. Lieut. L. B., gun-shot wound, left axilla, 24. iii. 18. Nerve found completely divided, 22. iii. 19.
Extension of the wrist produced by flexion of the metacarpo-phalangeal joints.

complete in all cases of hysterical palsy, it not infrequently happens that a most astonishing power to extend the wrist against gravity persists in cases of complete division of the musculo-spiral nerve above the supply of all the extensor muscles. The production of this extension is a true "trick" movement, for it is done by pulling on the tendons of the extensor communis digitorum by flexing the metacarpo-phalangeal joints with the interossei. As the metacarpo-phalangeal joints are flexed, the digital extensors are tightened, with the result that the hand is forcibly extended at the wrist joint (see fig. 3). It will be readily understood that in all cases of trick movements the detection of the trick is far more difficult than would be supposed from an inspection of a photograph of the action, the patient often possessing a subtle power to manipulate one joint while the observer's attention is directed to a neighbouring one.

(2) Although in a complete musculo-spiral lesion the metacarpo-phalangeal joints cannot be extended, it must not be forgotten that the two terminal phalanges may be straightened from the flexed position by the action of the interossei. This action is, at times, mistaken for musculo-spiral activity, and it is especially liable to cause confusion if the hand be examined whilst supported on a splint.

(3) The movements of the thumb in cases of division of the musculo-spiral nerve have proved deceptive in a very large number of cases. It is by no means uncommon for the patient to possess the power of extension in the terminal joint, or at times to show ability to extend the thumb at the metacarpo-phalangeal joint. In by far the greater number of these cases, the action is produced as a trick movement, the terminal joint being first bent by the flexor pollicis longus and then, when flexion is released, extension is produced by the passive pull of the long extensor. But in other cases the movement

Fig. 4. Complete division of the musculo-spiral. Rfm. F. O., gun-shot wound, upper third right arm, 23. i. 17. Nerve found divided, 3. ii. 19. No response when tested on table.
Extension of the thumb in complete musculo-spiral paralysis.

is more complex. It will be noticed that when the thenar muscles act upon the thumb, extension of the terminal phalanx is normally produced. This extension may be brought about by the passive pull of the extensor pollicis longus against the ulnar adductors of the thumb in the normal action. Or it may be done by a direct pull upon the sesamoid, and so upon the head of the metacarpal bone and front of the metacarpo-phalangeal joint. This pull tends to bring the metacarpal forward, and so create a relative extension of the last two joints.

In the patient illustrated at fig. 4 this was probably the case, since upon the left side this patient had a complete division of the ulnar as well as the musculo-spiral and was quite incapable of producing a movement in his left thumb like that illustrated in his right. At times it is possible that the abductor brevis may produce an active pull upon the expansion to the long extensor

tendon: but I do not think these cases are at all common. All movements of extension produced by the thenar muscles may usually be detected by the wriggling motion imparted to the metacarpo-phalangeal joint of the thumb; but it is not true, as is so commonly taught, that extension of the terminal joint cannot be produced, in cases of musculo-spiral paralysis, when the thumb is abducted, unless the precaution be taken that this abduction and immobilization affects both the metacarpal and the first phalanx.

D. *Complete division of the ulnar nerve*

(1) Paralysis of the flexor carpi ulnaris is particularly difficult to test. It is more easy to appreciate the voluntary action of this muscle in producing the movement of ulnar deviation of the hand, than by attempting to estimate its condition during active flexion of the wrist. There are probably few muscles in the body in which the apparently simple task of estimating voluntary action by observation and palpation, is so exceedingly difficult.

(2) The action of the interossei in producing adduction and abduction of the digits may be simulated by other muscles, and great caution is needed before statements are made as to recovery in ulnar nerve lesions on the strength of the patient showing some ability to spread the fingers apart and close them

Fig. 5. Complete division of the ulnar. Lieut. A. W., gun-shot wound, left elbow, 30. vi. 18. Test, 10. iv. 19, no response in ulnar intrinsics.
Abduction of all the fingers produced by the action of the long extensors. A, is the resting position of the digits—B, the position to which they can be abducted by the long extensors.

together again. It is a commonplace that as we open our hands with the extensors our fingers tend to spread apart, and as we close our fist with the flexors, our fingers are adducted. The movement of abduction effected by the extensors may be perfected in a very remarkable manner and it is not uncommonly mistaken for interosseus action (see fig. 5). It is to be noted that in true

interosseus abduction the fingers are all spread from the middle finger as a centre, but in extensor abduction this does not hold good, for the fingers are spread as a fan is opened and in the case photographed, the 4th digit remains more nearly at rest than the 3rd. The only satisfactory method of performing the test for interosseus action is to isolate each finger, and test its power of adduction and abduction to and from the middle line without permitting the long flexors or extensors to come into play. There are two additional points to be noted concerning the abducting power of the extensors.

(3) The extensor minimi digiti proprius is an exceedingly powerful abductor of the little finger. Its action may easily be mistaken for that of the abductor minimi digiti: and the fact that the little finger possesses this added mechanism of abduction accounts for the permanently abducted position which the finger takes up even long after the recovery of a sutured ulnar nerve (see fig. 6).

Fig. 6. Recovery after suture of the ulnar nerve; all ulnar muscles with completely recovered voluntary power.
Persistent abduction of the little finger caused by the action of the extensor minimi digiti and extensor communis digitorum.

(4) Although the extensor communis tendon to the index finger is able to produce abduction of the index in the general movement of extensor abduction, the extensor indicis proprius acts as a well-marked adductor. In the absence of any interosseus power, therefore, the index finger may be both adducted and abducted to and from the middle line (see fig. 7).

(5) The action of the long extensors upon the two terminal phalanges may prove a source of erroneous diagnosis. It has often been said that the action of the long extensors upon these two joints is but a feeble one; and recently it has been asserted very emphatically that not only have they no action whatever, but by the anatomical arrangement of their tendons, it is impossible that they should have any action. It is quite certain that the anatomical condition of the long extensor tendons, as properly displayed by dissection, is such as to permit extension of the two terminal joints of the fingers. It is equally certain that when the ulnar nerve is completely divided and the action of the interossei is entirely absent, the two terminal joints of the fingers

Fig. 7. Complete division of the ulnar nerve. Pte. W. R., gun-shot wound, left elbow, 17. iv. 18. Nerve found completely divided, 11. xii. 18. Test, 9. v. 19, no faradic or voluntary response in any ulnar muscle. Photo, May 1919.
Adduction of the index finger produced by the extensor indicis proprius. Abduction by extensor communis digitorum.

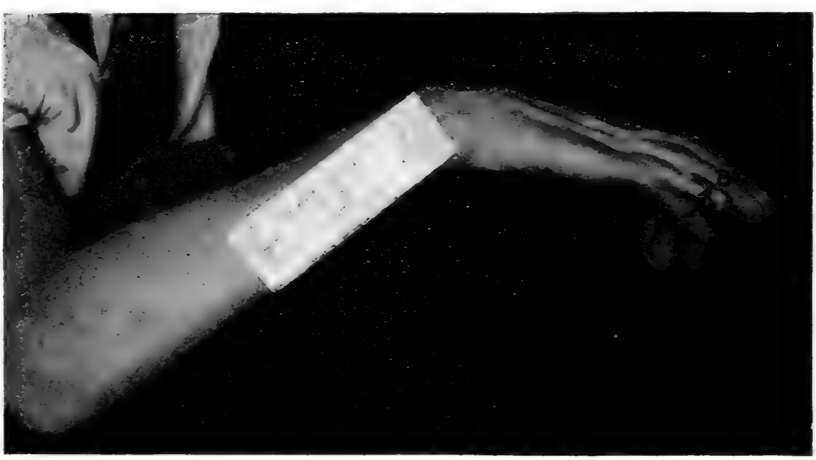

Fig. 8. Complete division of the ulnar nerve. Pens. C. H. H., gun-shot wound, right elbow, 21. x. 17. Nerve found completely divided, 26. iv. 19. Test, 26. iv. 19, no faradic or voluntary response in any ulnar muscle. Photo, May 1919.
Extension of the two terminal phalanges by the extensor communis digitorum.

can be extended by the action of the long extensors acting alone. This is not an abnormal action, it is one that can be witnessed in any case of division of the ulnar nerve, though the extension produced may not be so complete in all cases as in that illustrated at fig. 8.

(6) The statement that in complete ulnar lesions the metacarpo-phalangeal joints of the little and ring fingers cannot be flexed is, as a rule, incorrect. Although in the characteristic position of ulnar paralysis this joint in the little finger is extended, and the flexor digitorum sublimus has already produced a flexion of the first interphalangeal joint, nevertheless, a considerable degree of bending may be produced in the metacarpo-phalangeal joint by further action of the tendon of the flexor sublimus. In the ring finger, flexion of the metacarpo-phalangeal joint is readily produced by the flexor sublimus in cases of complete ulnar paralysis.

E. *Complete division of the median nerve*

(1) Several incorrect teachings concerning the failure to produce flexion in certain finger joints are current at the present time. The amount of paralysis that follows complete section of the median nerve is far less than would be imagined as the result of a study of anatomical text-books, and it is far less than that asserted by some observers of nerve injuries during the war.

(2) It is said that in cases of complete median interruption, the patient is unable to flex the second phalanges of any of the fingers. Flexion of the second phalanges, however, can readily be brought about by the flexor profundus *after* this muscle has bent the terminal joint. The second phalanges of minimus, annularis, and medius, can always be bent in complete median paralysis by the action of the intact flexor profundus (see fig. 10). The flexion produced is of a characteristic type, and may best be described as "winding up the finger."

(3) It is also asserted and emphasized by deductions from observations on the cadaver that the interossei cannot produce flexion of the metacarpo-phalangeal joints; these joints being bent by the action of the lumbricales only. This teaching is absolutely wrong, and it has led to the very incorrect diagnostic criterion that in median nerve paralysis the metacarpo-phalangeal joints of index and medius cannot be flexed. Every case of complete division of the median nerve has power to flex the metacarpo-phalangeal joints of these fingers, and the flexion in these cases is produced, as it is in the normal subject, by the action of the interossei, although, of course, the lumbricales assist in the action (see fig. 9).

(4) The common statement that the distal phalanges of index and medius cannot be flexed, needs very careful qualification. If the index finger be grasped, and the patient is told to bend the top joint of that finger only, no action of flexion is produced. If the same test be applied to medius, a definite flexion movement can usually be evoked. But if the patient is merely asked to bend the fingers, or especially if he is asked to make a fist, then some flexion of all joints

of all the fingers is produced. In some cases a very fair fist may be made in cases in which the median nerve is completely divided (see fig. 10). Evidently,

Fig. 9. Complete division of the median. Pte. C. W., gun-shot wound, left arm, 10. iv. 18. Median found divided, 17. vii. 18. No voluntary or faradic response in median muscles, 26. iv. 19.
Flexion of index and medius at the metacarpo-phalangeal joints.

Fig. 10. Complete division of the median. Pte. A. H., gun-shot wound, right arm, 21. iii. 18. Nerve found divided, 21. ix. 18. No voluntary or faradic response in median muscles, 12. v. 19.
Ability to make a fist with the median divided above the supply of the long flexors of the digits.

if the volition is a general one, the main action of the flexor digitorum profundus brought about by the route of the ulnar nerve is sufficient to produce a flexion of all the fingers. But if the volition is merely limited to the exclusive

median portion destined for the index finger, then no contraction of the muscle takes place.

(5) Flexion of the terminal joint of the thumb is sometimes possible in median nerve lesions in which the long flexor is paralysed. The flexion, though definite, is not complete, and is stamped by that characteristic inability to operate in the presence of any resistance which usually accompanies movements produced by relaxation of opponents.

(6) Flexion of the metacarpo-phalangeal joint of the thumb has been said to be impossible without the action of the muscles innervated by the median nerve: but the ulnar muscles inserted to the ulnar sesamoid are capable of producing this movement, and in this instance, as in the next two to be examined, we have an example of the almost utter impossibility of diagnosing lesions of the nerves supplying short muscles of the thumb merely by looking

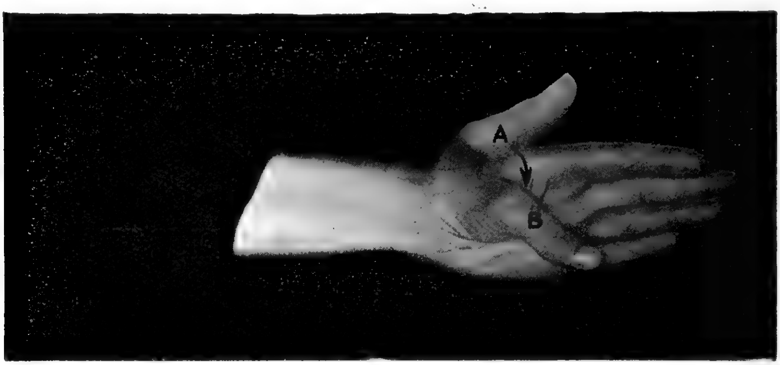

Fig. 11. Complete division of the median. Pte. C. W., gun-shot wound, left arm, 10. iv. 18. Nerve found divided, 17. vii. 18. 26. iv. 19, no faradic or voluntary response in any median intrinsic muscle.
Opposition of the thumb in complete median paralysis.

at the movements of which the thumb is capable. Electrical tests and careful palpation of the thenar muscular mass are essential preludes to a diagnosis.

(7) It is best to state quite dogmatically at the outset that the complex combination of muscular movements which gives effect to the volition of opposing the thumb to the other digits, is often perfectly carried out in cases of complete division of the median nerve (see fig. 11). In performing this action, some muscle is needed to pull the metacarpal bone of the thumb in a palmar direction, another muscle is required to move the thumb towards the ulnar side of the palm, and to complete the process of perfect opposition some muscle is required to produce a rotation of the thumb. The extensor ossis metacarpi pollicis produces a forward movement of the metacarpal bone, and in the production of opposition in cases of median paralysis the part played by this muscle is generally apparent. When the thumb is pulled in a palmar direction, the adductor pollicis will produce the ulnar sweep, and,

with effective opposition from the extensor ossis, will also produce a deceptive degree of rotation of the thumb. In many cases in which the movement of opposition is quite perfect, that part of the adductor obliquus muscle which is inserted to the radial sesamoid effects a rotation not to be distinguished from true opponens opposition as in the case illustrated in fig. 11. Digital examination of the metacarpal of the thumb will reveal the atrophy of the opponens in these cases, but mere inspection of the movements produced may not be taken by any anatomist or any clinician as evidence of median recovery.

(8) The loss of the abductor pollicis in median paralysis is often extremely well compensated by the power of the extensor ossis metacarpi pollicis to pull the whole thumb in a palmar direction. A good deal of reliance has been placed on the "abduction test" in cases of median paralysis: but in a certain

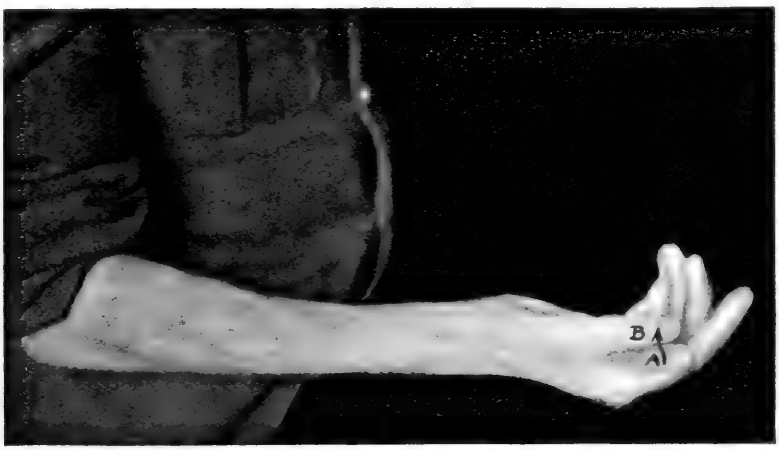

Fig. 12. Complete division of the median. Nerve divided for pain, 20.ii.19. No recovery, 26.v.19.
"Abduction" movement of the thumb produced by extensor ossis metacarpi pollicis.

number of cases this spurious abduction brought about by a muscle innervated by the musculo-spiral nerve is a very well defined and forcible action, though naturally its range of movement is never so great as in that produced by the abductor brevis (see fig. 12).

F. *Complete paralysis of both median and ulnar nerves*

(1) It is in this condition that the typical "ape hand" is developed. The essential features of this hand are the flatness of the palm, and the rotation of the thumb in a direction opposite to that produced by the opponens (see fig. 13). The thumb ranges itself alongside the index finger with its palmar surface directed in a palmar direction, in the same manner as the remainder of the digits. It is rather curious that the production of this position

of the thumb is ascribed by Benisty[1] to the action of the adductor pollicis—a muscle which is of necessity paralysed in these cases.

The muscle which produces this movement in the thumb is the extensor pollicis longus which is thus, as regards rotation of the thumb, the opponent of the opponens.

Fig. 13. Complete division of ulnar and median nerves. Pte. J. B. *Typical position of the thumb produced by the rotating action of the extensor pollicis longus unopposed by the intrinsic thenar muscles.*

Fig. 14. Complete division of both ulnar and median. Pte. A. B., gun-shot wound, right arm, 10. iv. 18. Both nerves found divided, 11. vi. 18. No recovery, 26. v. 19. *Flexion of the fingers produced by extension of the wrist.*

(2) One very curious and deceptive action seen in some cases is that illustrated in fig. 14. Although all the finger flexors are completely paralysed, distinct and forcible flexion, which enables the patient to scratch with the finger nails, and to close the hand, is readily carried out. This trick action

[1] *Clinical forms of nerve lesions*, 1918, pp. 55 and 116.

is exactly the opposite to that mentioned in those cases of musculo-spiral paralysis in which the wrist may be raised by bending the fingers; for here the bending of the fingers is effected by raising the wrist.

(3) An action which has led to more confusion in diagnosis than probably any other, is that power of wrist bending which is normal to the extensor ossis metacarpi pollicis. The movement of the wrist produced by this muscle is illustrated in fig. 15, and in this case the action effected against gravity is a forcible one, although under these conditions its range is not very great.

G. *Nerve lesions of the lower extremity*

In the leg there are but few voluntary muscular actions which are likely to deceive, but it may be said at once, that if voluntary power is examined for with the patient lying on his back with his heel resting on the couch,

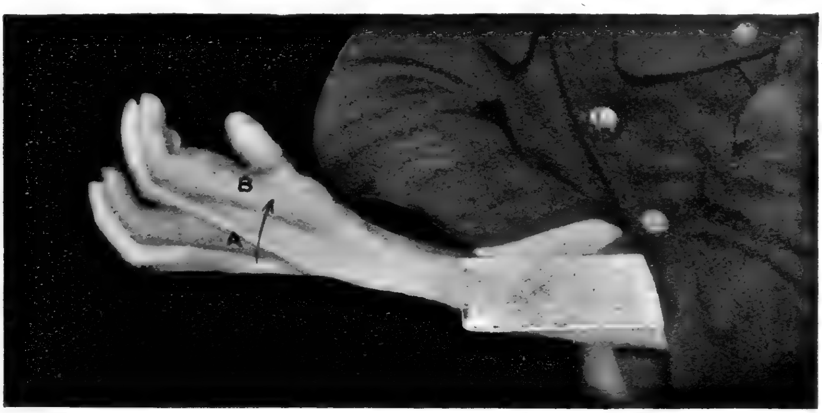

Fig. 15. Complete division of ulnar and median. Pte. A. R., gun-shot wound, left axilla, 19. vii. 18. Both nerves found divided, 13. xii. 18. No faradic or voluntary response in any median or ulnar muscle, 5. iv. 19.
Flexion of the wrist produced by the extensor ossis metacarpi pollicis.

almost any conclusion may be arrived at. The patient has only to push or to pull against his heel as a fixed point to produce movements of his foot in either direction; and this push or pull may be effected by any muscle capable of taking a leverage from the couch.

(1) The action of the peronei as elevators (dorsi-flexors) or depressors (plantar-flexors) of the foot has been somewhat debated. In the first place, the peronei belong to the external popliteal group of muscles and their normal action on the foot is to produce eversion. Eversion is itself a movement of greater possibilities in the position of dorsi-flexion. But it has often been said that anatomically the peronei—or some of them—are muscles which produce plantar-flexion. There is no doubt that in the normal condition the peronei act with their group, and come into play during dorsi-flexion of the foot. Suppose, however, the internal popliteal nerve is completely divided and the

calf muscles are paralysed, will a movement of plantar-flexion be produced by the peronei? In the great majority of patients there remains no power to depress the foot under these conditions, for the peronei, even if anatomically capable of prodúcing plantar-flexion, cannot be dissociated in their action from the remaining muscles, supplied by the external popliteal, which produce dorsi-flexion. But, at times, the patient possesses the power of contracting the peronei without contracting the other external popliteal muscles;—he can dissociate the action of the peroneus group. In these cases plantar-flexion, and eversion is the result; and if the action be not carefully studied, it may be mistaken for evidence of internal popliteal recovery (see fig. 16). One might therefore say that normally the peronei were muscles which do not act upon the ankle joint, but which produce eversion of the foot usually in a position

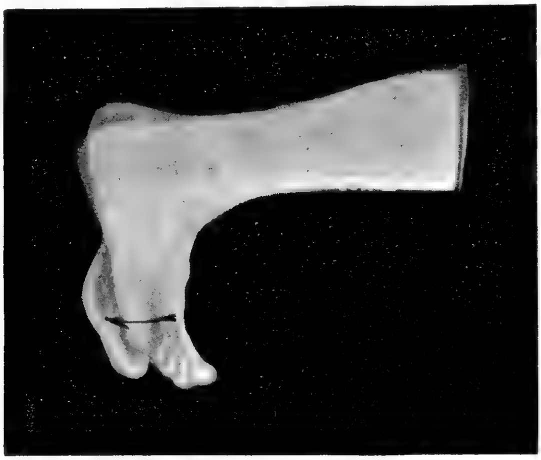

Fig. 16. Complete division of the internal popliteal; verified, 30. v. 19.
Action of the dissociated peroneii muscles.

of dorsi-flexion, but that occasionally, in cases of internal popliteal paralysis, they may be dissociated by the patient from the remainder of their group and be used as plantar-flexors when they act alone. This is a case of the volition demanding plantar-flexion finding in some persons an agent not usually employed in this service.

CONCLUSIONS

The purpose of this paper is to emphasize the fact that estimating the condition of injured nerves by the study of the voluntary movements of which the patient is capable, is an extremely difficult, and at the best, somewhat uncertain business. That the re-education of muscles, in cases of nerve injury, is a matter requiring far more anatomical knowledge than is often brought

to bear upon it; since without proper care it will certainly result in the education of trick movements which, when perfected, are accepted as evidences of recovery. That much of the teaching upon muscular action which has been put forward from a study of nerve lesions during the war is erroneous.

Finally that anatomists should exercise great caution before authoritative sanction is given to teaching which may lead to false estimates of the damage done to nerves, and the recovery of nerves after operation; since on the one hand operation may be negatived or delayed, and on the other operative procedures which are futile may be encouraged, or legitimate operations may be estimated as having an unreal success. In either case that period which marks the transition from the sphere of activity as a serving soldier to that of useful civil employment may be very much prolonged. When, as during the war, the problem affected the welfare of thousands, it behoves anatomists to exercise an attitude far more judicial—far more critical—than has been evidenced up to the present time.

I wish to express my indebtedness to Major-General Sir Robert Jones and to Major Rowley Bristow for the opportunities for clinical investigation that form the basis of this paper.

SEXUAL DIFFERENCES IN THE SKULL

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MORE than a year ago one of us worked out the average contours of 30 male and 30 female, eighteenth century, skulls from the Clare Market district, though there was then no time to work out or call attention to the sexual points of difference between them.

As a matter of fact there was no way of being sure how far they were rightly sexed because few anatomists have the chance of testing their capabilities in this way on a series of skulls of known sex.

Still we propose to take the two series of tracings as a starting point and to see whether any of the differences between them are repeated in other series.

In the first place, on comparing the two norma verticalis tracings (fig. 3), it is evident that the female skull is shorter and broader in proportion than is the male, and it is no surprise to find that its cranial index is 775 while that of the male is 755. As it is obviously an important point to settle whether any definite allowance should be made for sex in comparing different groups of skulls we looked up the records of the other series of English skulls lately measured and found them as follows:

Hythe	♂ 79·9	♀ 81·9
Rothwell	♂ 76·3	♀ 75·8
Moorfields	♂ 75·5	♀ 75·0
Whitechapel	♂ 74·3	♀ 73·1

The results of this investigation were not very encouraging; Hythe showed the same preponderance of 2 per cent. in the female index noticed in the Clare Market series, but in the other three groups the males had a larger index than the females. We felt therefore that it was essential to get some material where the sexing was not the arbitrary work of an expert whose personal equation was unknown, even to himself, and we turned to the records of Anglo-Saxons because, as they are generally buried with male or female weapons and ornaments, there is much less chance of mistaking the sex than in later English burials.

22 male Saxons gave us an index of 74·3, and 23 females one of 75·3.

Later on, Dr Duckworth of Cambridge helped us very much by sending us records of 160 bodies from the dissecting room on which both the head

and the skull measurements had been taken and in which, of course, there was no doubt of the sex.

The cranial index of 120 male skulls was 75·8 and of 40 female 78·2.

As we were unable to get any more series the sex of which was definitely known except the series of soldiers at Millbank in which there were no females for comparison, we had recourse to the living head and measured 150 male medical students at St Thomas's Hospital and 150 female students at the Medical School for Women.

This, of course, brought us up against the allowance which it is necessary to make for the soft parts in comparing the living head with the bare skull.

Until lately craniologists have followed the example of Miss Lee in allowing 11 mm. for these, but Dr Gladstone found that a little over 7 mm. was sufficient, while Dr J. H. Anderson suggested 9 mm.

Our method of testing the thickness of the covering tissues was to run a needle through a thin disc of cork, the needle was then stuck into the scalp until it touched the bone, when the cork was moved down to the skin; then the needle was withdrawn and the distance between the cork and its point measured.

This method was so simple that a large number of records could be obtained in London post-mortem rooms in a short time and we soon had ample evidence that 8 mm. was a good allowance for the soft parts in both the length and breadth of the skull. This is the more satisfactory in that it is midway between Gladstone's and Anderson's results.

With regard to height, it is not enough to allow for the thickness of the tissues on the vertex and in the roof of the external auditory meatus, because in a dried skull the ear plugs of the auricular craniometer are in quite a different position to that they occupy with the soft parts in place; they are much nearer together in the skull and the removal of the soft parts may merely allow them to approach one another while their centres still occupy the centre of the canal. Another point which has to be taken into account is that the cartilaginous meatus is rising as it passes inward.

In practice we found that scraping the soft parts out of the bony meatus until the plugs could occupy the position they would take in the dried skull made a difference on the average of 1·5 mm. and this we attributed largely to the slope of the meatus. We would therefore suggest allowing 5·5 mm. for the difference in height between the living head and the dried skull, 4 mm. for the scalp and 1·5 for the meatus. This is rather less than Anderson suggests but is somewhere very near the average.

In practice it will be found that the change from the cranial to the cephalic index means an addition of 1 per cent.

Another comparison available was between the male and female patients in St Thomas's Hospital whom we may regard as representative of the modern migratory Londoner of the lower and lower middle class, while a still further one was between the male and female visitors to the British Association's

meetings as quoted by Dr Macdonell. These probably would represent pretty much the same class of society as the male and female medical students; that is to say, perfectly nourished individuals interested in intellectual occupations.

If we now tabulate the results of these (with the possible exception of the Anglo-Saxons) definitely sexed series we get the following:

			Excess of ♀ index
Anglo-Saxons	♂ (22) 75·9	♀ (23) 76·3	0·4 per cent.
London Medical Students	♂ (150) 78·7	♀ (150) 79·5	0·8 ,,
Cambridge Dissecting Room	♂ (120) 78·01	♀ (40) 79·6	1·6 ,,
London Patients	♂ (50) 77·7	♀ (50) 79·3	1·6 ,,

It seems therefore that all the material which has not been subjected to arbitrary sexing agrees in giving the female heads a higher index than the male by about 1 per cent., and if this ratio should be confirmed in the future we may have in it a useful method of checking the correctness of our endeavours in sexing unknown collections of skulls[1].

The next point is to determine whether the female skull has increased its index by decreasing its length or increasing its breadth in proportion to the male and for this the length and breadth averages are necessary.

	L.	Br.	L.	Br.
London Med. Students	♂ 193·4	152·3	♀ 185	147
British Association	♂ 198·1	155	♀ 185·6	148·3
Cambridge Dissecting Room	♂ 194·3	151·5	♀ 186	148
London Patients	♂ 193·3	150	♀ 182·4	144·7
Clare Market	♂ 196	150	♀ 186	146

In other words, among the London Medical Students the length of the ♀ head is 95·1 per cent. of that of the male while the breadth is 96·5 per cent.

In the British Association	length is	93·7	per cent.
,, ,,	breadth is	95·7	,,
In the Cambridge Anatomy School	length is	95·7	,,
,, ,,	breadth is	97·7	,,
In the London Patients	length is	94·4	,,
,, ,,	breadth is	96·5	,,

It will therefore be seen that in all these separate groups the ratio of the breadth of the female is 2 per cent. nearer that of the male than is the length, or, in other words, that there is a 2 per cent. greater loss of length than of breadth in the female English skull compared with the male.

Having traced the sexual difference to the length it naturally became a question whether it might not be accounted for by the greater development of the frontal sinuses in the male and the only means of checking this which occurred to us was to take the ophryo-maximal measurements and see whether

[1] Since writing the above we are interested to note that Fleure and James found the same increase of the cephalic index in the female sex in Wales. *Journ. Anthrop. Inst.* 1916, p. 48.

there was the same proportional difference between the sexes that was noticed in the glabello-maximal; the argument being that, as the ophryo-maximal length only affects the brain containing part of the skull while the glabello-maximal represents brain and air, any difference in the proportion of the two lengths to the breadth must be due to a difference in the air containing part.

In the large series of skulls at Hythe which one of us measured (*Journ. of Anthrop. Inst.* vol. XXXVIII. p. 419) it was found that the difference between these two lengths was, on an average, 2 mm. for male skulls and nothing at all

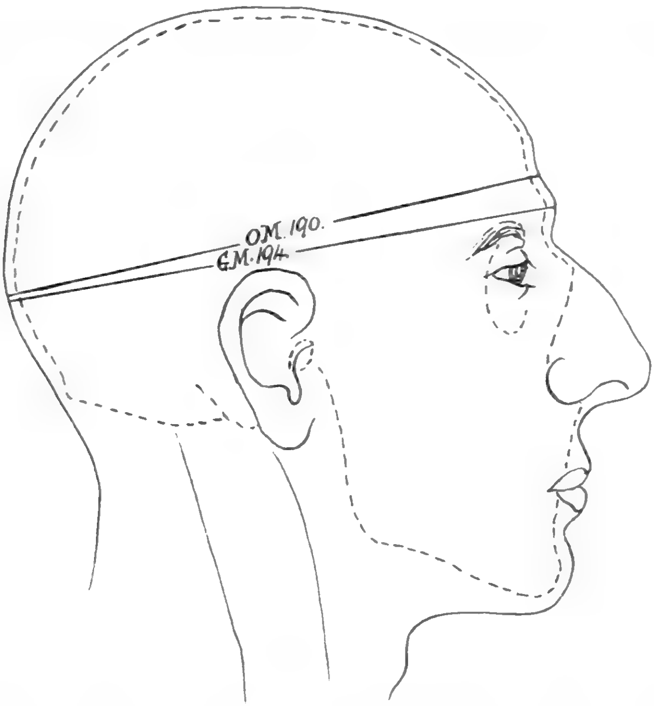

Fig. 1.

for the female. We have repeated the measurements on 100 patients in St Thomas's Hospital, 50 males and 50 females, with the same result.

Assuming that this difference is approximately accurate, we find that, if we deduct 2 mm. from the glabello-maximal length of the 150 St Thomas's Hospital male students' heads, the length of the 150 Women's School students is 96·65 per cent. of the St Thomas's length and the breadth 96·5 per cent. In other words that the female heads were 3·5 per cent. smaller than the male in both the antero-posterior and transverse diameter. This is exactly what we were looking for because on removing the 2 mm. due to air, the proportions between length and breadth become the same in the two sexes and so the cephalic index becomes the same.

When we came to the other series, however, the results were not so satisfactory from this point of view, but the simplest thing will be to tabulate the four sets of results.

	♀ shorter than ♂	♀ narrower than ♂
London Medical Students	3·5 per cent.	3·5 per cent.
London Hospital Patients	4·5 ,,	3·5 ,,
Cambridge Dissecting Room	3·3 ,,	2·3 ,,
British Association	5·4 ,,	4·3 ,,

From this it appears that the subtraction of 2 mm. from the male length does not equalize the proportions of length and breadth except in one series out of four. The other three agree in requiring another 1 per cent. removed from the male in order to equalize the cephalic index in the two sexes.

The amount is not great, but it is worth noticing, and our available material makes us think that the average English female skull is slightly broader, in proportion to its length, than the male even when the increased size of the air sinuses in the latter is allowed for.

One has, of course, to think whether there is any reason why the medical students should not have fallen into line with the other series, and the only one we can suggest is that they were all young adults in whom, perhaps, the sinuses were not as well developed as in the older groups.

On Checking the Sexing of Skulls

As all the different series of skulls in which the males and females were known agree in showing the female head as 2 per cent. broader than the male in relation to its length it appears that we have a check on the accuracy of the arbitrary sexing of those large series in which the sexes are not known.

Judged in this way the following results are interesting:

		♀ index > ♂	♀ index < ♂
(30 ♂ 30 ♀)	Clare Market	2 per cent.	
	Hythe	1·5 ,,	
	Moorfields		·6 per cent.
	Whitechapel		·3 ,,
	Rothwell		·5 ,,

The Clare Market and Hythe series therefore answer our expectations well enough, but the other three show the reputed males with a higher cephalic index than the females, a condition of things which is not in harmony with the evidence at present before us and makes us regard their accurate sexing as probably not very happy.

The Facial Index

On comparing the norma facialis tracings of the two sexes in the Clare Market series it will be seen that the males have an average length of 121 mm. from the nasion to the lower chin level against 116 mm. in the females while the greatest bizygomatic breadth is 129 mm. in the males against 123 mm. in the females. This means that the proportion of the length to the

breadth of the face or facial index is 93·8 in the male against 94·3 in the female. This, of course, is in the dried skull and we do not know any other collection of skulls, either accurately or tentatively sexed, with which to compare this because in all the collections we know the lower jaws are missing. We are, therefore, thrown back upon living faces with all the difficulties of adequate allowance for soft parts.

After careful examination of sections of faces we suggest 8 mm. as an ample allowance for the soft parts in the breadth and 4 for those in the length, and this would make the living Clare Market index 91·2 for the males and 91·6 for the females.

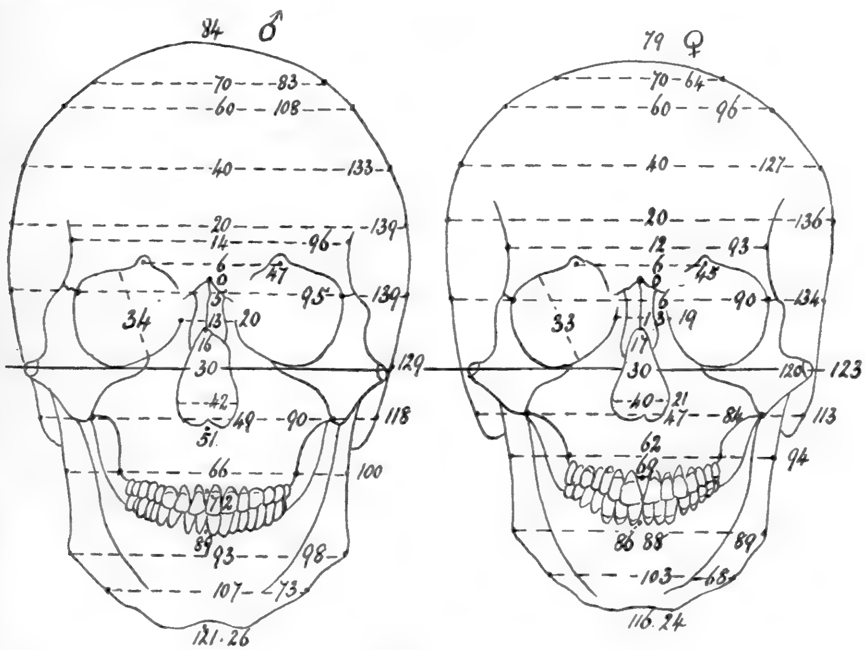

Fig. 2.

Against this we have to set 53 male students of St Thomas's Hospital with an index of 870 and 100 female students from the Women's School with one of 863, which means that while the Clare Market female facial index is practically equal to the male, the living female students' index is 99·2 that of the male students.

This makes us doubt whether any use can be made of the facial index for sexing purposes, and our work, so far, is negative from this point of view.

The Breadth-height Index

The difference in the appearance of the cranial vault is rather striking when the norma facialis of the two sexes is viewed side by side and suggests a difference in the breadth-height index. If this index is to be checked in the living head it will be necessary to use the auricular height which may be

ascertained by taking the height of the vertex above the Frankfurt plane and adding 6 for half the external auditory meatus.

This gives 120 mm. for the males and 115 for the females, and, when the maximal breadth is divided by it, the index is 84·5 ♂ and 83·3 ♀. This difference in the index means that the female skull has lost 4·2 per cent. of the male height but only 2·8 of the male width.

At present we have little material definitely sexed with which to compare this, but as far as 103 male and 25 female medical students go we find the proportion is the same because the male breadth-height index is 89·3 and the female 88·2.

This is the cranial index, not the cephalic, obtained after deduction of 8 mm. from the breadth and 5·5 mm. from the height.

Bimolar Width

Professor Keith has lately called attention to the diminution in the width of the palate in modern English compared with Saxon skulls; here we are only concerned with sex and it is striking how much narrower the female palate is than the male. The distance between the maxillary tuberosities in the males is 62 mm. while in the females it is 54 mm., and it will be noticed that the same line which joins the tuberosities is continued on to the lower jaw. In the maxillary width the female skull is 8 mm. narrower than the male, but in the wider mandibular width in the same line the female is only 6 mm. less than the male. Unfortunately we are unable to check this record at present on certainly sexed material.

Zygomatic Width

The Bizygomatic width or face breadth has been considered already in connection with the facial index and we now wish to consider it from the norma verticalis in connection with the width of the cranium.

In looking at this norma it is evident that the male skull is a good deal more phaenozygous than the female and the question arises whether the zygomata are more splayed in the male or whether the vault of the skull is fuller in the female in the anterior part of the temporal fossa. We shall probably get a better idea of this if we compare the bizygomatic width with the maximal skull breadth rather than with the inter-stephanic width.

If we do this we find that the zygomatico-maximal index or proportion of the zygomatic width to the maximal width is 90·9 per cent. in the male, and 87·0 per cent. in the female. This indicates that the zygomatic arch is distinctly wider in relation to the skull width in the male than in the female. We were able to check this in the male and female medical students in whom the male index was 89·7 per cent. and the female 88·5 per cent. These observations were made on 53 male and 100 female students.

Apparent tapering forward of the Skull

Apart from the difference in zygomatic width the male skull appears to taper away in the anterior temporal region much more than the female does;

in other words that the pterionic region in the female is fuller than in the male. A useful measurement is to our hand in the breadth taken a quarter of the way back along the length of the skull. This in the male is 115 and in the female 112. Contrasting these with the maximal width we get an index of 81 in the male and of 81·2 in the female.

This index suggests that the appearance of fulness is illusory and due to the feeble development of the zygomata in the female.

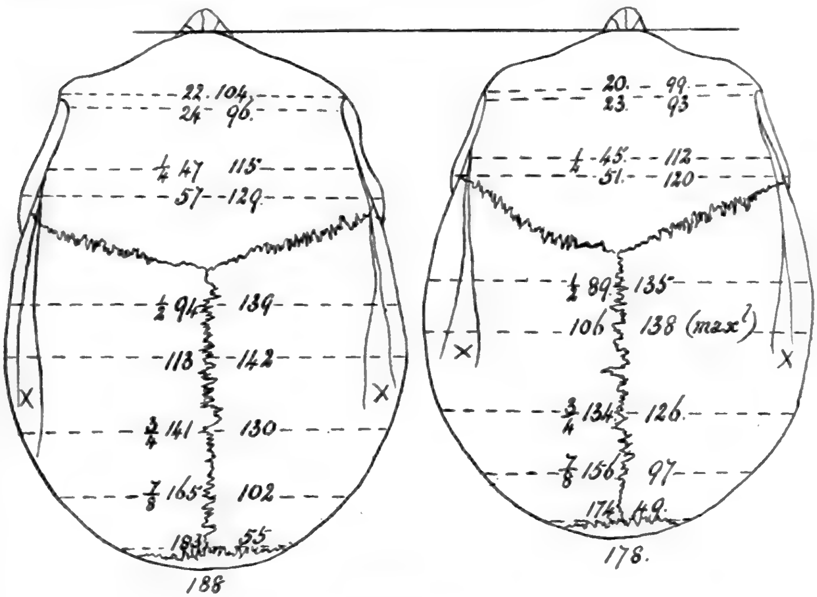

Fig. 3.

CONCLUSIONS

From the material at present at our disposal we have come to the following conclusions about the English skull.

1. That the female skull is shorter in proportion to its breadth than is the male by 2 per cent. and that this difference is not fully accounted for by the greater development of the frontal sinuses in the male.

2. That in those series of artificially sexed skulls in which this proportion is markedly departed from the sexing has probably been unsuccessful.

3. That the facial index does not differ in the two sexes.

4. That the female skull is lower in proportion to its width than the male, by from one to two per cent. when the auricular height is taken.

5. That the female skull is some 8 mm. narrower in the width of the palate than the male.

6. That the zygomatic arches are wider in proportion to the maximal breadth of the skull by 4 per cent. in the male than in the female.

THE ILEO-CAECAL REGION OF *CALLICEBUS PERSONATUS*, WITH SOME OBSERVATIONS ON THE MORPHOLOGY OF THE MAMMALIAN CAECUM

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The material on which this note is based consisted of three specimens of the South American monkey, *Callicebus personatus*, and one specimen each of *Dasypus sexcinctus*, *Tatusia novemcincta* and *Cyclothurus didactylus*, which were collected by the Percy Sladen Expedition to Brazil in 1913 and which were placed at my disposal by Professor J. P. Hill, to whom I desire to express my indebtedness and my thanks.

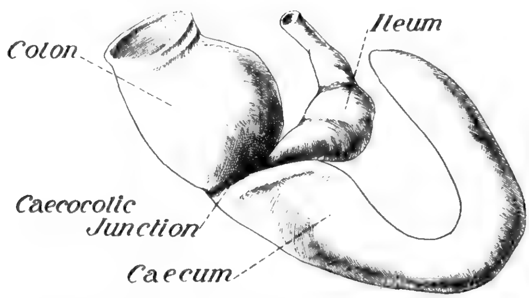

Fig. 1. Ileo-caecal region of *Callicebus personatus*. Ventral surface.

External appearances. In each case the commencement of the colon was distinctly dilated, although the length of gut involved was not constant, being 4 cm. long in two cases and 8 cm. long in the third—the "caecal colon" of Keith (1). The succeeding portion of the gut was in a state of tonic contraction for a distance of 8 cm. in the two former specimens and for 2·5 cm. in the third specimen. The term "caeco-colic sphincteric tract" has been suggested by Keith (6) for this portion of the large gut. From this point onwards to the anal canal, the colon showed a series of sacculations, each separated from its neighbour by a firmly contracted portion, varying from ·5 cm. to 1 cm. in length.

Only two taeniae coli could be made out. They were situated, the one on the dorsal surface and the other on the ventral surface of the colon near the mesenteric border, but their edges were not sharply demarcated.

The Caecum, which occupied the right iliac fossa, was demarcated from the colon by a circular depression which passed downwards and medially across the gut (fig. 1). In each of the three specimens it was distended and its capacity was rather greater than that of the stomach. In none did it contain gas. Its conformation was different in each case. In one (fig. 1), it was about 12 cm. long, and was curved to the left in a U-shaped manner. In another, it was 15 cm. long and formed a flat coil of one and a half turns. In the third, it was 16 cm. long and formed a spiral coil of one and a half turns, the commencement of the second turn of the spiral passing dorsal to the first turn. In each case it was clear that growth had been greater along the anti-mesenteric than it had been along the mesenteric border of the gut and that the coiled condition had resulted from an earlier U-shape.

The anterior and posterior vascular folds of Huntington (2) were present and the artery contained in the latter was in two of the three specimens the longer vessel and extended to the apex of the caecum.

In each case the caecum gradually tapered from its commencement to its apex, and in no case were taeniae coli distinct on its surface.

The Ileum terminated in the right iliac fossa by passing upwards and laterally into the medial aspect of the colon, where its entrance was marked on the surface by a V-shaped furrow (fig. 1). It was closely applied to the wall of the caecum.

Internal appearances. The mucous membrane of the commencement of the colon was smooth except on its dorsal wall where a few longitudinal corrugations were present.

The ileum protruded into the colon for ·5 cm. and its mucous membrane was thrown into ridges parallel to its long axis. The upper lip of the opening was quite distinct but the lower lip was not so salient owing to its relation to the caeco-colic valve.

The caecum was separated from the colon by a well-developed *caeco-colic valve*, annular in shape with a central opening and so placed that the plane of its aperture was directed upwards and medially. The valve was widest at the medial side of the gut, where it lay immediately below the termination of the ileum. The mucous membrane on both of its surfaces was thrown into radiating ridges (fig. 2), and, on the medial side, these ridges were directly continuous with the longitudinal ridges of the ileal mucous membrane. On the lateral side of the gut the caeco-colic valve was in the same plane as the upper lip of the ileo-colic valve, but, owing to the obliquity of its peripheral attachment, which corresponded to the depression on the outer surface (fig. 1), on the medial side it lay immediately below the lower lip of the ileo-colic valve. In this situation it hung downwards towards the caecum, presenting a spout-like appearance (fig. 2).

Over the ventral surface and along the anti-mesenteric border of the caecum, the mucous membrane was smooth, but longitudinal corrugations were strongly marked over the dorsal surface and along the mesenteric border.

At the base of the U (fig. 1), two prominent transverse corrugations were present on the mesenteric border of the gut.

No lymphoid patches were recognisable in the ileo-caecal region on naked-eye examination.

Microscopical appearances. The upper or colic lip of the ileo-colic valve was, as is usual, covered on its outer surface with mucous membrane typical of the large intestine and on its inner surface with mucous membrane typical of the small intestine. The circular muscle coat of the latter was prolonged into the substance of the valve, but the circular coat of the large intestine ended abruptly at the base of the valve, where the longitudinal muscle fibres met and interlaced without becoming continuous with one another and without entering into the formation of the valve.

Sections through the lower or caecal lip of the ileo-colic valve also passed through the caeco-colic valve on the mesenteric border of the gut. The circular

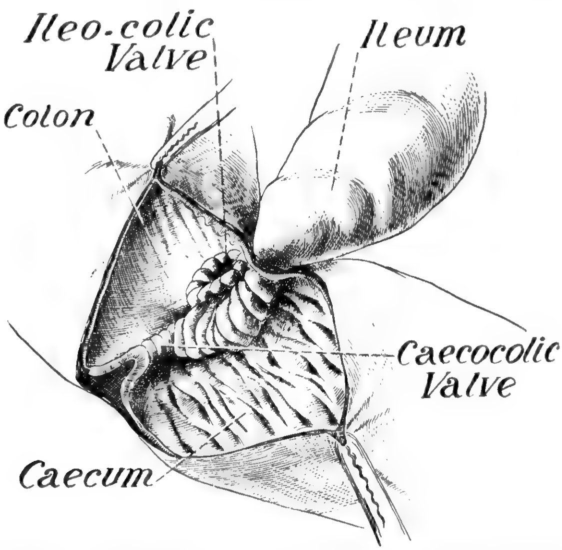

Fig. 2. Ileo-caecal region of *Callicebus personatus*. A window has been made in the wall of the gut so as to expose the ileo-colic and caeco-colic valves.

muscle coats of the ileum and caecum lay side by side, separated only by a few longitudinal fibres of the caecum and by some connective tissue, for some distance from the ileal termination. On separating from one another, that of the ileum entered the ileo-colic while that of the caecum entered the caeco-colic valve. The mucous membrane corresponded in its arrangement with the circular muscle coats. The villi disappeared at the apex of the lip of the ileo-colic valve and the mucous membrane, where it was associated with the circular muscle coat of the caecum, assumed the characteristic features of the large intestine.

The caeco-colic valve was covered on both colic and caecal surfaces by

mucous membrane typical of the large intestine, which was loosely connected with the underlying muscle. The entire thickness of the circular muscle coat of the colon passed into the substance of the valve, as did that of the caecum, so that the valve contained two layers of circular muscle fibres which became continuous near its free margin. These two layers carried in with them on their outer surfaces a fine layer of longitudinal fibres derived from the longitudinal muscle coats of the colon and caecum respectively. These fibres could only be traced into the middle of the valve and, thereafter, the two layers of circular muscle fibres were only separated by connective tissue (fig. 3).

The majority of the longitudinal muscle fibres of the colon were directly continuous with the longitudinal muscle fibres of the caecum.

The caecal wall showed no difference in structure throughout the whole of its extent, i.e. the mucous membrane near the apex was indistinguishable

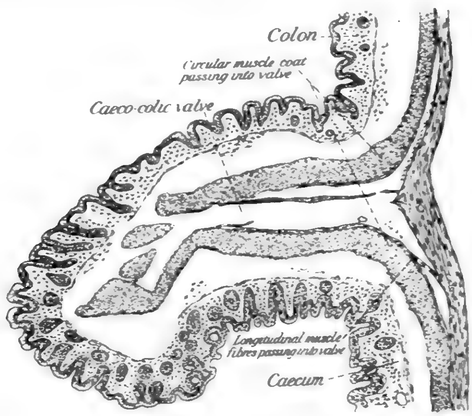

Fig. 3. Longitudinal section through the anti-mesenteric border of the gut at the junction of the caecum and the colon of *Callicebus personatus*, to show the structure of the caeco-colic valve.

from the mucous membrane of the rest of the caecum. Small nodules of lymphoid tissue were found in the submucous tissue but they were not more numerous near the apex than elsewhere.

Particular observations. The size of the caecum of *Callicebus personatus* relative to the size of the stomach and the presence of a competent caeco-colic valve constitute strong evidence that in this genus the caecum has a definite function to perform in connection with the process of digestion. The thickness of the circular muscle coat in the valve indicates that it acts as a powerful and efficient sphincter, and it is probable that the longitudinal fibres which enter into its constitution provide a muscular means of relaxation.

Fig. 3 shows clearly that the muscular core of the valve is not produced by a localised thickening of the circular muscle coat of the gut, but constitutes a true infolding of the whole thickness of that coat, a condition similar to that described by Sappey (3) in the spiral intestinal valve of Raja. Owing to the

obliquity of the peripheral attachment of the valve, many of the circular fibres which are found in it laterally, must, as they are traced medially, leave the valve and re-enter the wall of the colon, ultimately reaching the medial wall of the gut on the same level as the upper or colic lip of the ileo-colic valve. It would seem, therefore, to be not improbable that the contraction of these fibres approximates the lateral part of the caeco-colic valve to the upper lip of the ileo-colic valve, in this way causing the ileum to open into the caecum through the oblique inlet of the former. As already pointed out, the medial part of the caeco-colic valve is in intimate relation with the lower lip of the ileo-colic valve and its spout-like appearance suggests that the contents of the ileum may pass directly into the caecum.

The condition of the vascular folds of the caecum corresponds to what Huntington (2) described for the closely allied *Ateles ater*, namely that either the ventral or the dorsal fold and its contained artery may be the longer. It may be stated that the external appearances of the ileo-caecal region of *Callicebus personatus* and *Ateles ater* are very similar, but I have not had an opportunity of examining the internal and microscopical appearances of the latter.

As compared with the ileo-caecal region of *Callicebus personatus*, the condition found in the old-world monkey presents some manifest differences.

In a specimen of *Cercopithecus aethiops* which I examined, the stomach possessed a capacity eight or ten times greater than that of the caecum, which was, relatively, much smaller than the caecum of *Callicebus personatus*. The shape of the caecum in all the old-world monkeys is attributable to the fact that growth along the anti-mesenteric border of the gut has been in excess of the growth along the mesenteric border. Thus, in *Cercopithecus aethiops*, the caecum is U-shaped.

In all the old-world monkeys, the proximal part of the caecum is sacculated and these sacculations—produced in the same way as the sacculations in other parts of the colon—are separated from one another by deep furrows, which do not, however, pass completely round the gut, being absent at the mesenteric border. It follows that taeniae coli are well marked on the caecum in its proximal part. In *Callicebus personatus*, on the other hand, the sacculations are absent and the taeniae coli are not distinct.

In the old-world monkeys the terminal tapering of the caecum is abrupt, unlike the condition found in *Callicebus personatus*, but the diminution in calibre is not sufficient to justify its identification as a vermiform process.

The arrangement of the peritoneal folds in *Callicebus personatus* has been described on p. 67. In *Cercopithecus aethiops* the intermediate non-vascular fold is very well developed and forms a large triangular fold which occupies the angle between the terminal part of the ileum and the medial wall of the proximal part of the caecum. The anterior and posterior vascular folds, however, are very short so that the vessels they contain run practically on the gut wall.

In the specimen of *Cercopithecus aethiops* which I examined, the ileo-colic

valve was found to be directed tailwards, i.e. towards the caecum, and the terminal part of the ileum passed posteriorly and laterally into the colon. The specimen had been preserved in formalin and I believe that the condition was probably brought about by post-mortem and abnormal muscular contraction. At the same time it is clear that the particular muscular contraction which produced the condition after death may be able to produce the condition during life.

In the interior of the caecum of *Cercopithecus aethiops*, the furrows separating the sacculations on the outside formed definite folds containing circular muscle fibres. These folds may have acted as a sphincter for the caecum, but they were not continued all round the gut; they were produced by the difference in length between the longitudinal and the circular muscle coats; and they did not constitute a true caeco-colic valve.

If the condition of the ileo-caecal region of the new- and old-world monkeys be compared with the condition found in the anthropoid apes, it will be found that the increased growth along the anti-mesenteric border of the caecum is the most striking characteristic which all three groups possess in common.

The small size of the caecum relative to the stomach, the possession of definite taeniae coli and the corresponding caecal sacculations, and the absence of the caeco-colic valve are characters which the anthropoid shares with the old-world monkey.

On the other hand, the anthropoid differs both from the old- and the new-world monkeys in possessing a vermiform process. It also possesses both an intermediate non-vascular ileo-caecal fold and a well developed dorsal vascular fold[1].

It will be seen, therefore, that so far as the ileo-caecal region is concerned, the old-world monkeys are much more closely allied to the anthropoids than are the new-world monkeys.

It may be of some interest to point out that, as regards both the caecum and the caeco-colic valve, *Tarsius tarsius*, which Wood Jones (14) excludes from the Lemurs, closely resembles *Callicebus personatus*.

General observations on the mammalian ileo-caecal region. In human anatomy, the term caecum is used to denote that portion of the large intestine which lies on the proximal side of the ileo-colic valve. In comparative anatomy, the term is not always used to describe the same morphological entity. The caecum of the monkey corresponds exactly to the human caecum, but the caecum of the rabbit, the horse and some other mammals includes, in addition, the proximal part of the colon proper. This difference is not always borne in mind, but Keith (6) believes that the proximal part of the colon proper should be regarded as functionally part of the caecum and he terms it the "caecal colon." He has indicated that he considers that the "caecal colon"

[1] The morphology of these folds is fully discussed by Huntington (2).

is morphologically the primitive vertebrate caecum and that the diverticular blind end appears at a later stage in phylogeny.

In the present paper consideration is being restricted to the morphology of the *caput caecum coli* of human anatomy, and I would be content to draw attention to the risk of confusion in nomenclature and to point out that the "caeco-colic valve," which Sisson (4) describes in the horse, is not identical with the caeco-colic valve of *Callicebus personatus.*

The frequent occurrence of a competent caeco-colic valve is overlooked by Chalmers Mitchell (5) when he makes the following statement: "The normal caecum of mammals, however, always appears to be a forward continuation of the hind-gut, the one cavity being directly continuous with the other in the simplest fashion, except in those cases in which it is slightly complicated by vestiges of the presence of the second caecum of an original pair." It is not possible to regard the caeco-colic valve as a vestige of the presence of the second caecum of an original pair, even if one agreed with the author in his view that the primitive mammalian caecum was a paired structure. When it is remembered that the caeco-colic valve is a true sphincter of the caecum, that amongst mammals it is sometimes present, sometimes replaced by an intra-colic valve, and sometimes completely absent it will be evident that its value as an aid in studying the morphology of the caecum is by no means negligible.

In opposition to currently accepted ideas, Keith (6) has put forward the view that the human caecum is not in a state of retrogression. He regards the commencement of the colon, which is usually found to be dilated, as a feeding chamber for the caecum, the passage of the chyme being effected by anti-peristaltic waves, which Cannon (7) and Barclay Smith (8) have described. Keith points out that the portion of the colon immediately beyond the dilatation is very commonly found tonically contracted in mammals and in birds, and he looks upon it as a sphincter for the caecum and "caecal colon." Consequently he has suggested the term "caeco-colic sphincteric tract" to denote it and he believes that, in man, the upper part of the ascending colon represents this tract and functions as a sphincter for the human caecum. He draws attention to Berry's (9) work on the vermiform process in support of his view that the human caecum is an actively functioning part of the alimentary canal.

Annular valves, very similar to the caeco-colic valve of *Callicebus personatus*, are found in the alimentary canals of many fishes and reptiles, and are clearly very primitive in type, but they are none the less competent and efficient in their action. Many of Keith's observations were made on the rat and he has himself referred to the presence of a caeco-colic valve which he has figured. He does not explain, however, why, in the presence of a competent valve, a "caeco-colic sphincteric tract" should be necessary, nor does he explain why, if a sphincter is required, a tonically contracted tube should take the place of a primitive annular valve. The "caeco-colic sphincteric tract" would appear to be destined, like the oesophagus and the human de-

scending colon, to act as a passage for the rapid conduct onwards of incoming contents, and not as a sphincter.

Huntington (2) has drawn attention to the fact that "representatives of all the main types of ileo-colic junction are found within a very limited zoological range, as within the confines of a single order...differences in the method of nutrition have impressed their influence on the structure of the alimentary canal and have led to the evolution of varying and divergent types of ileo-colic junction." This is an indication that the possibilities of variation are limited, and I believe that they are very much fewer than Huntington lays down. Asymmetry in origin and asymmetry in growth are the outstanding characteristics of the mammalian caecum, and I believe that the primitive mammalian caecum was asymmetrical, i.e. a diverticulum derived from the anti-mesenteric border of the colon just beyond the ileal termination, such as is found in some reptiles, e.g. *Pseudemys elegans*, *Eunectes marinus*, etc. As the caecum enlarged and its functional activity increased, a caecal sphincter was developed. Further caecal progress necessitated the redistribution of, or increase in, the lymphoid tissue, with the consequent appearance of the vermiform process. Variations of diet led to retrogressive changes in form. Retrogressive changes at an early stage may account for the complete absence of the caecum in *Dasyurus viverrinus*. Retrogressive changes at a later stage may account for many of the reduction forms found in carnivora. Finally, retrogressive changes imposed on the most advanced form may account for the reduction in size accompanied by the retention of the vermiform process found in the wombat, the anthropoid apes and man.

Wood Jones (14) has recently put forward a somewhat unorthodox view of the morphology of the caecum. "The human vermiform appendix," he says, "although usually regarded as a particularly degenerated rudiment, is strangely like that of such simple creatures as some of the pouched animals of Australia, and the very different structure found in the monkeys is most likely a specialisation from a primitive condition which is retained in man." From this one might with some justice infer that the author believes that the simpler the animal, the more primitive the type of the caecum, but, as Huntington has shown, all the main types are to be found within the limits of a single order. The conception that such a caecum as that of *Callicebus personatus* or of *Cercopithecus aethiops* has been derived from a condition similar to that found in man and the anthropoid apes is one for which I am unable to find any supporting evidence. On the other hand, I have tried to show that the vermiform process is present in two types of caeca. In the one, the caecum is relatively large and obviously plays an important part in the digestive process and this increased functional importance demands a redistribution of the lymphoid tissue, which is manifested by the presence of the vermiform process.

In the other, the caecum is relatively small, it possesses no true sphincter, its wall is sacculated—a common condition in large, actively functioning caeca but uncommon in relatively small caeca, which do not possess a vermiform

process—and its general characters are such as to suggest strongly that it is a reduction stage of the first group.

Retrogressive changes necessarily are associated with loss of function and the caecal loss of function will be indicated in the first place by the disappearance of the sphincteric valve.

I therefore conclude that, in the determination of the phylogeny of a given caecum, the condition of the caeco-colic valve is of the greatest importance.

In putting forward this suggestion as to the primitive mammalian caecum, I am aware that it is in agreement neither with the conception of Huntington (2) nor yet with that of Chalmers Mitchell (13). The former refers all mammalian caeca to a primitive vertebrate type with no caecum, and he derives the various types found to-day in different ways from a condition similar to that found in *Echelus conger*.

Chalmers Mitchell (13) believes that the single mammalian caecum is the persistent member of a primitive pair of caecal appendages, homologous with the paired caeca of birds. He compares the paired caeca of birds and the paired caeca of the little ant-eater, *Cyclothurus didactylus*—which are both laterally placed—with the paired caeca of *Petaurus sciurens*, in which the large caecum is anti-mesenteric in position and the (?) vestigial caecum is connected to the mesenteric border of the gut, and he states that any anatomist would agree that the structures involved are the same.

This statement would only be justified if the author had brought forward evidence to show how caeca, which were previously lateral in position, came to be situated on the anti-mesenteric and mesenteric borders of the gut, and, in the absence of such justification, one cannot concede that the paired lateral caeca of *Cyclothurus didactylus* are identical with the so-called paired caeca of *Petaurus sciurens*.

If, therefore, we exclude the paired caeca of *Petaurus sciurens* and other forms where the larger structure—usually accepted as the caecum—is anti-mesenteric in position, there still remain certain mammals which have been described by Flower (10), Owen (11) and other observers as possessing paired lateral caeca. The list includes the armadilloes, *Dasypus sexcinctus*, *Dasypus villosus* and *Tatusia novemcincta*, the little two-toed ant-eater, *Cyclothurus didactylus*, and the *Manatee* (Chalmers Mitchell).

The *Manatee* possesses a bifid caecum, springing from the anti-mesenteric border of the gut, and can be excluded as an example of the paired lateral caeca.

In *Tatusia novemcincta*, the condition at the ileo-colic junction is described differently by different authors. Huntington cites it as an example of the symmetrical type of ileo-colic junction, with median transition of the ileum and, although he does not definitely make the statement, it can be inferred that he, like Flower (10), regards the caecum as being absent. Chalmers Mitchell on the other hand describes the same animal as possessing small paired globular caeca. Both these authors agree in believing that the "paired lateral caeca"

of *Dasypus sexcinctus* and *Dasypus villosus* constitute an advanced stage of the condition found in *Tatusia novemcincta.*

Examination of the ileo-colic junction of Tatusia, when the gut is empty, is sufficient to satisfy the observer that growth along the anti-mesenteric border of the commencement of the colon has been definitely greater than it has been along the mesenteric border (fig. 4). Further, the longitudinal muscle coat of the ileum passes continuously on to the anti-mesenteric border of the colon and there constitutes a definite taenia coli. This does not occur on the lateral aspects of the ileo-colic junction, and I believe that the condition represents a well-marked transition stage between the condition where the ileum is in direct linear continuity with the colon, and the condition which Huntington describes as the right-angled type of ileo-colic junction. I regard the dilatation on the anti-mesenteric border of the commencement of the colon as the true caecum. When the colon of Tatusia is artificially distended the lateral wall of the commencement of the colon tends to bulge, and these two bulgings are separated from one another by the anti-mesenteric taenia coli already referred to. These bulgings are regarded by Chalmers Mitchell as paired lateral caeca, but I prefer to regard them as the first stage in the production of a bifid caecum.

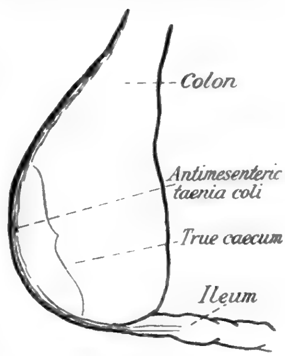

Fig. 4. Ileo-caecal region of *Tatusia novemcincta*, ventral surface showing anti-mesenteric taenia coli and asymmetrical ileo-colic junction.

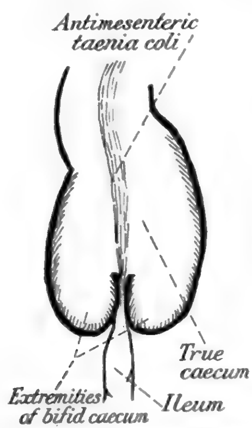

Fig. 5. Ileo-caecal region of *Dasypus sexcinctus* showing anti-mesenteric aspect with well-marked taenia coli separating the two extremities of the bifid caecum.

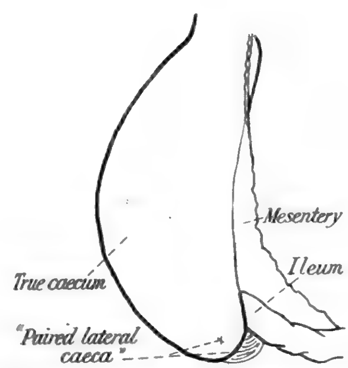

Fig. 6. Ileo-caecal region of *Dasypus sexcinctus* showing asymmetry which indicates the true caecum.

This view is strongly confirmed by the condition found in *Dasypus sexcinctus*. In this animal the anti-mesenteric taenia coli and its continuity with

the longitudinal muscular coat of the ileum are very striking (fig. 5). The colon is asymmetrically dilated at its commencement—the true caecum (fig. 6)—but further growth of the anti-mesenteric border of the gut has been modified, because the taenia coli has not kept pace. As a result *Dasypus sexcinctus* possesses "paired lateral caeca" which I regard as a typical unpaired caecum with a bifid extremity, and a modification of this caecum may, with justice, be believed to be the origin of the bifid caecum of the *Manatee*.

There remains for consideration the condition found in the little two-toed ant-eater, *Cyclothurus didactylus*, of which Hunter (12) says: "There are two caeca as in birds." Flower's (10) description is as follows: "The colon is short and is very remarkable for having at its commencement a symmetrically disposed pair of short caeca, narrow at the base, and rather dilated at their terminal blunt end, and communicating with the general cavity by very minute apertures."

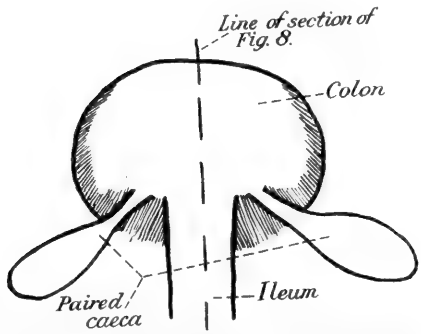

Fig. 7. Ileo-caecal region of *Cyclothurus didactylus*, ventral view showing the "paired lateral caeca."

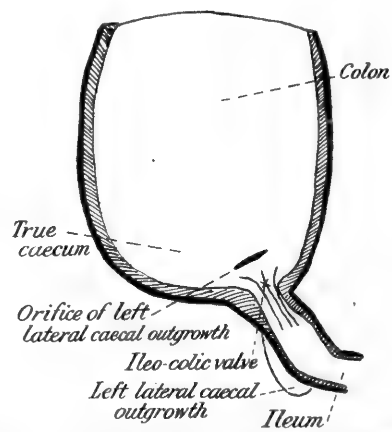

Fig. 8. Sagittal section through ileo-caecal region of *Cyclothurus didactylus* along line shown in Fig. 7. The asymmetrical ileo-colic transition is shown and the position of the true caecum is indicated.

Huntington (2) classes it as a more advanced stage of the condition found in *Dasypus sexcinctus*, but the caeca of these two animals show very striking differences. In Dasypus, as already noted, the paired caeca are separated from one another only by the anti-mesenteric taenia coli. In Cyclothurus, their attachments are very widely separated (fig. 7). In Dasypus, the caeca are of a size in conformity with the size of the colon, whereas in Cyclothurus they are relatively very small. In Dasypus, the caeca are widest at their connection with the colon; in Cyclothurus, they are very narrow at their colic ends, but dilated and bulbous at their blind extremities, a curious condition to which Flower (10) has drawn attention.

A sagittal section through the ileo-colic junction of Cyclothurus (fig. 8) shows the same asymmetrical transition as has been already pointed out in

Tatusia novemcincta, and a similar degree of increased growth along the anti-mesenteric border of the colon.

Transverse sections through the stalk or proximal part of the caecal outgrowth show that the mucous membrane is thick and vascular and that the lumen is relatively small. In the distal two-thirds, the lumen is much larger but the mucous membrane is not so thick. A complete longitudinal muscular coat is present throughout, as in the vermiform process of other animals. Unfortunately, in the specimen examined by me the material had not been fixed with a view to microscopical examination, and I am therefore unable to describe the appearance of the mucous membrane, beyond saying that it appeared to conform to the type usually found in the caecum.

Consideration of the differences which have been enumerated above leads me to regard the paired lateral caecal outgrowths as new formations and the dilatation at the commencement of the anti-mesenteric border of the colon (fig. 8) as the morphological caecum.

It is clear therefore that the paired caeca can be explained in such a way as to bring them into line with other mammalian caeca and that they do not constitute an insurmountable obstacle to the acceptance of the views which have been put forward in this paper.

CONCLUSIONS

1. The caecum of *Callicebus personatus* is an actively functioning part of the alimentary canal.
2. The caeco-colic valve is the true caecal sphincter.
3. Where the functional caecum does not correspond to the morphological caecum, e.g. in the horse, the rabbit, etc., the caeco-colic valve is replaced by an intra-colic valve.
4. The human caecum, which possesses no competent caeco-colic or intra-colic valve, is in a condition of retrogression.
5. The primitive mammalian caecum was an asymmetrical structure derived from the anti-mesenteric border of the colon immediately beyond the ileo-colic junction by increased growth over a localised area.
6. The paired lateral caeca of *Dasypus sexcinctus* and *Dasypus villosus* are regarded as the extremities of a bifid caecum.
7. The paired lateral caeca of *Cyclothurus didactylus* are new formations and do not correspond to the morphological caecum.

At the same time, one recognises that much valuable information, which has still to be obtained with regard to the comparative embryology of the caecum, is not yet available and that it may therefore be necessary to modify one's views in the light of subsequent knowledge.

I desire to express my thanks to Mr G. L. Birbel, who is responsible for figs. 1 and 2, and to Miss Muriel Sutton, B.Sc., who is responsible for fig. 3, for the care and trouble which they have taken over these drawings.

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ON THE DEVELOPMENT OF THE LARYNGEAL MUSCLES IN SAUROPSIDA

By F. H. EDGEWORTH, M.D.

In a paper published in 1916 I showed that in the pig the laryngeal muscles, other than the Crico-thyroid, are developed from the Constrictor oesophagi. In this paper evidence is given that the laryngeal muscles of the Sauropsida have a similar derivation.

Reptiles. The laryngeal cartilages of Reptiles (vide Henle and Göppert) consist of a cricoid, and two arytenoid cartilages articulating, or continuous, with it. The musculature consists of a Dilatator laryngis and a Constrictor laryngis. Laryngei are present in some cases.

These muscles were considered by Göppert (1899) to be homologous with those of Amphibia, and like them, to be derived from branchial muscles.

As far as I know, no description has hitherto been given of the development of the cartilages or of the muscles.

Hochstetter (1908) stated that in Reptiles (Emys lutaria, Anguis fragilis, Tropidonotus, Lacerta agilis) the lungs are developed from paired lateral or ventro-lateral grooves of the epithelial lining of the oesophagus. At their anterior ends they communicate by a transverse bifurcation groove, whilst in front of this and continuous with it a median ventral groove develops. The pulmonary sacs grow backwards from the hind ends of the pulmonary grooves. The bifurcation and branchial grooves are folded off from the oesophagus, from behind forwards.

Schmidt (1913) stated that in embryos of Calotes, Mabuia, and Ptychozoon, the lungs are developed from the oesophagus, as paired diverticula at the junction of its lateral and ventral walls. The trachea is developed later, behind the branchial region, as a shallow median groove in the floor of the oesophagus. It extends backwards and soon joins the transverse bifurcation groove which unites the pulmonary diverticula. In Calotes and Mabuia, though most marked in the former, there are two tracheal grooves, of which the left becomes the permanent groove, whilst the right gradually disappears by being taken up into the left groove. The tracheal groove subsequently extends forwards into the pharyngeal region, the epithelium in the median line of the floor of the pharynx thickening into a plate. Meanwhile the separation of the trachea from the oesophagus proceeds cranially, right up to the solid epithelial plate. The breaking through of the tracheal lumen into the pharynx was not observed—it occurs later. The solid epithelial plate corresponds in position to the larynx.

The development of the laryngeal muscles was followed in Chrysemys marginata and Tropidonotus natrix.

In a 6 mm. embryo of Chrysemys (figs. 1–3) the open tracheal groove extends from the bifurcation groove, 180 μ behind the 5th gill-clefts, forwards to 80 μ behind them. In front of this the oesophagus has a more oval shape. The oesophagus and tracheal groove are surrounded by cells of uniform appearance and no indication of oesophageal or laryngeal muscles is visible.

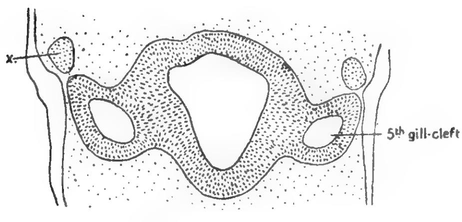


Fig. 1.

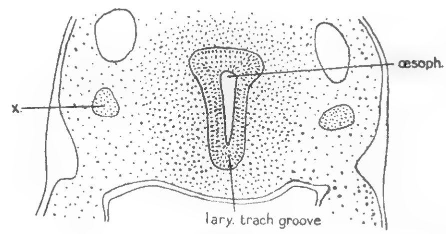


Fig. 2.

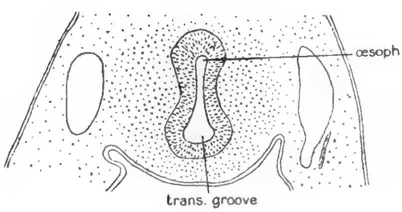


Fig. 3.

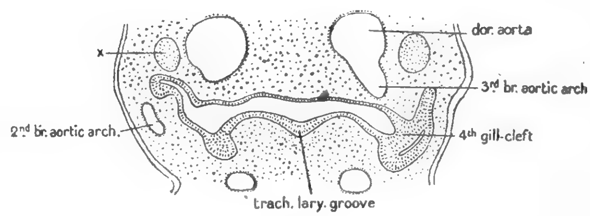


Fig. 4.

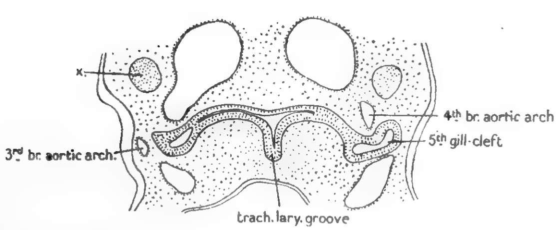


Fig. 5.

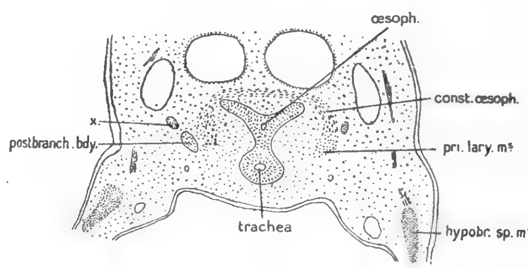


Fig. 6.

In an embryo of 7 mm. (figs. 4–6) the tracheo-laryngeal groove begins 140 μ behind the 5th gill-clefts, and is continued forwards to the level of the 4th gill-clefts; it is a deep groove in the oesophageal region and at the level of the 5th gill-clefts; it then becomes wider and shallower and is barely marked at the level of the 4th gill-clefts. The trachea behind the bifurcation groove and the tracheo-laryngeal groove are surrounded by aggregated mesoblast cells—the first indication of the laryngo-tracheal skeleton. The forepart of the oesophagus is surrounded, dorsally and laterally, by the ∩-shaped primordium of the Constrictor oesophagi and laryngeal muscles.

In an embryo of 8 mm. (fig. 7) the primordium of the laryngeal muscles has separated on either side from the Constrictor oesophagi. It extends from 170 μ behind, to the level of, the 5th gill-clefts. The recurrent laryngeal nerve passes towards it.

In an embryo of 9 mm. (figs. 8–10) the tracheo-laryngeal groove extends from 100 μ behind the 5th gill-clefts to the level of the 4th gill-clefts. The tracheal lumen is continued forwards to the level of the 5th gill-clefts. The primordium of the laryngeal muscles extends from 140 μ behind the 5th gill-clefts to the level of the 4th gill-clefts.

From this time onwards the increasing curvature of the embryo made another method of measurement necessary. In an embryo of 8·1/2 mm. crown-rump length—slightly more advanced than one of 9 mm. in total length—there is but little change. The tracheo-laryngeal groove begins 50 μ behind, and the laryngeal-muscle-primordium 90 μ behind, the 5th gill-clefts.

In an embryo of 12 mm. crown-rump length (figs. 11–14) the trachea has altogether separated from the oesophagus, so that the laryngeal epithelium is continuous only with that of the branchial s. pharyngeal region, from the level of cornu branchiale i to that of the cornu hyale. The laryngeal muscles lie solely in the branchial s. pharyngeal region. Their primordium, on each side, has separated into the lateral half of the Constrictor laryngis and the Dilatator laryngis. The former meets its fellow in the mid-dorsal and mid-ventral lines. The latter lies external to the Constrictor.

In an embryo of 15 mm. (figs. 15–16) crown-rump length the ventral surface of the Constrictor is attached to the Basibranchiale. The cricoid and arytenoids form a continuous, slightly chondrified mass, which is continuous posteriorly, with the tracheal skeleton.

In Tropidonotus the younger embryos have a cork-screw form so that measurements of length were not possible, and the stages described are arbitrarily named.

In stage (i), the earliest available (figs. 17–20), the continuity of the tracheo-laryngeal with the oesophago-pharyngeal epithelium extends from 30 μ behind the 5th gill-clefts to the 4th gill-clefts. The primordium of the laryngeal muscles, just separated from the Constrictor oesophagi, extends from 90 μ behind to the level of the 5th gill-clefts. The recurrent laryngeal nerve passes to its hind end.

In stage (ii) (figs. 21–22) the continuity of the laryngeal with the pharyngeal epithelium extends from the 2nd to the 1st gill-clefts, i.e. is only in the 1st branchial and hyoid segments. The primordium of the laryngeal muscles extends from the 3rd to mid-way between the 2nd and 1st gill-clefts.

In an embryo of 3 cm. the condition of the laryngeal skeleton and laryngeal muscles is identical with that in a 6 cm. embryo, except that chondrification has not taken place.

In a 6 cm. embryo (figs. 23–27) the larynx is raised in a median projection

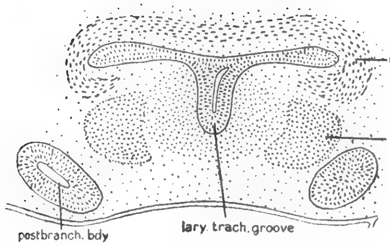
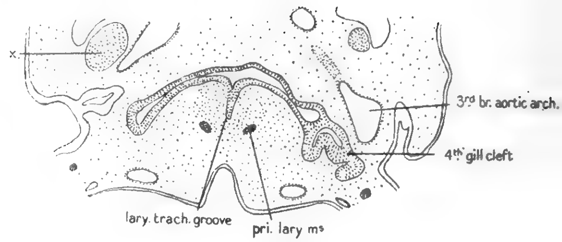


Fig. 7.



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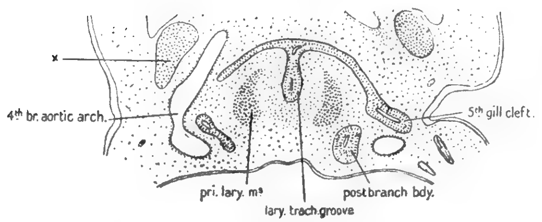

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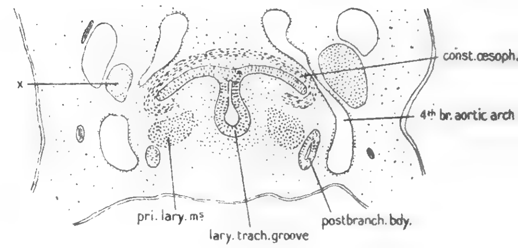

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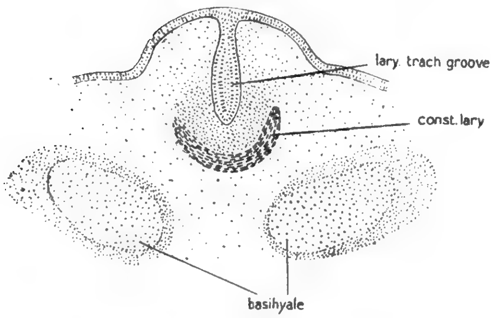

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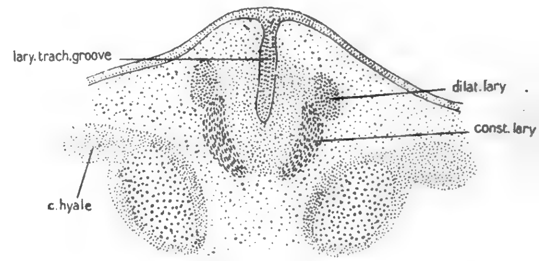

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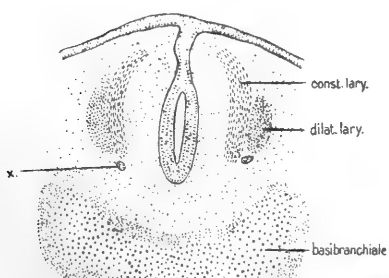
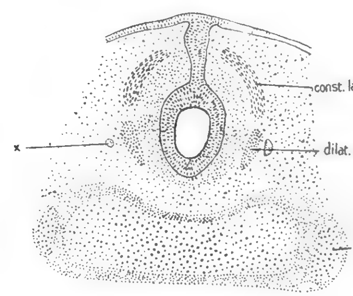


Fig. 13.



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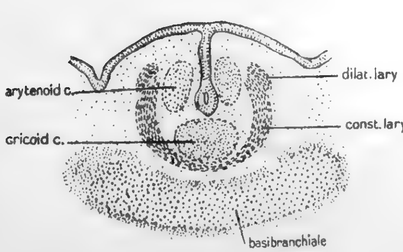
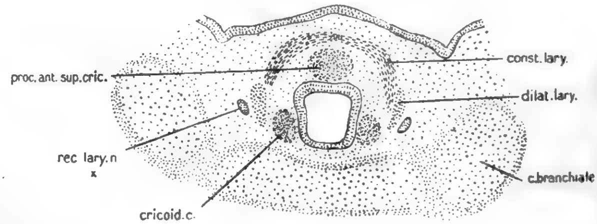


Fig. 15.



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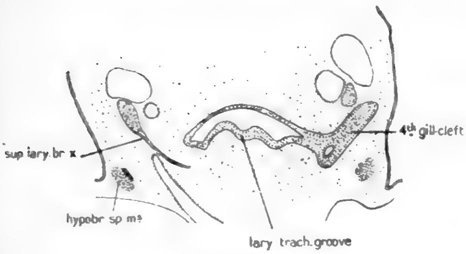

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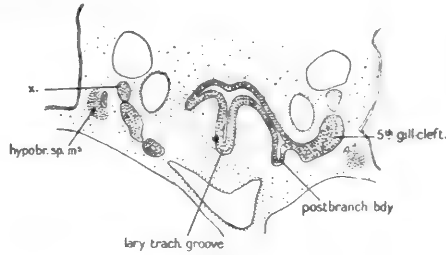


Fig. 18.

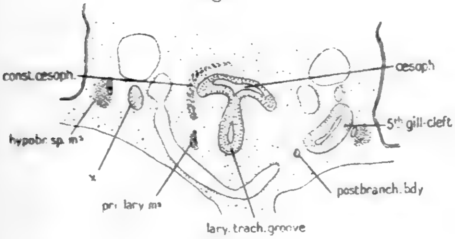


Fig. 19.

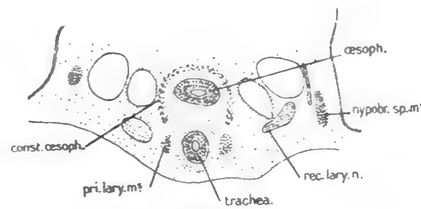
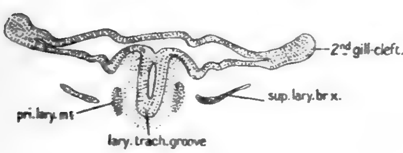


Fig. 20.



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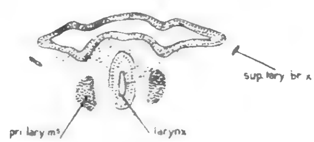

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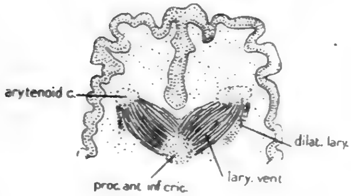

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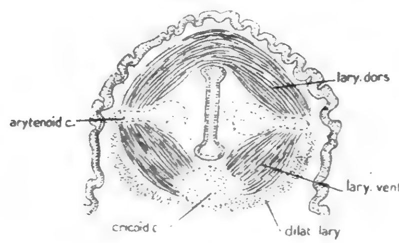

Fig. 24.

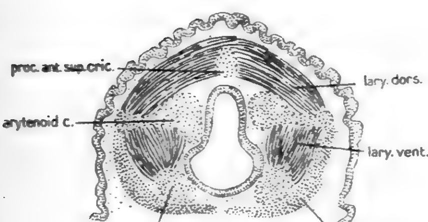

Fig. 25.

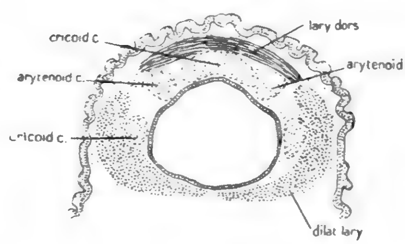

Fig. 26.

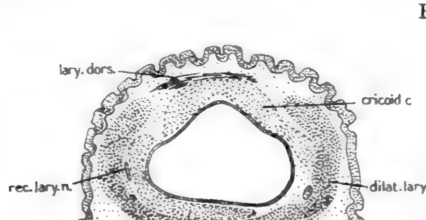

Fig. 27.

of the floor of the mouth overlying the tongue. The laryngeal and tracheal skeleton forms a continuous whole and is chondrified. The cricoid has median superior and inferior processes projecting from its front edge. The arytenoids are continuous with the cricoid. The primordium of the laryngeal muscles has separated into the Laryngei dorsalis and ventralis and the Dilatator. The Laryngeus dorsalis arises partly from the dorsal surface of the cricoid and from its anterior superior process and is partly continuous with its fellow across the middle line without any raphé; it is inserted into the dorsal surface of the arytenoid. The Laryngeus ventralis arises from the sloping upper edge of the cricoid and from its anterior inferior process; it is inserted into the ventral surface of the arytenoid. The Dilatator arises from the side of the trachea and from the cricoid, passes forwards and slightly upwards and is inserted into the external edge of the arytenoid.

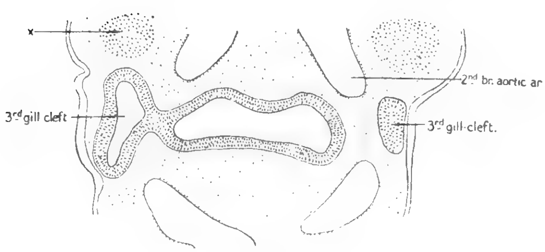

Fig. 28.

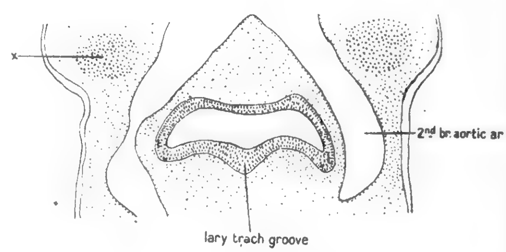

Fig. 29.

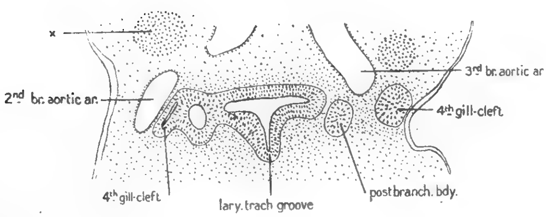

Fig. 30.

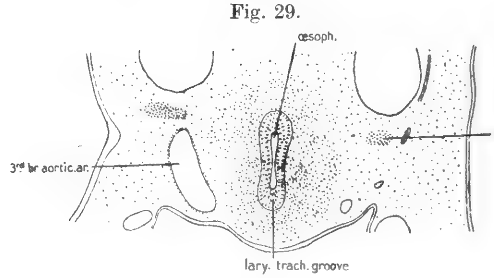

Fig. 31.

Birds. Weber and Buvignier stated that in the duck the primordia of the lungs develop as paired ventro-lateral diverticula of the oesophagus, and the laryngo-tracheal canal later, as a median ventral groove of the oesophageal wall; in the fowl the pulmonary and laryngo-tracheal primordia develop simultaneously.

This was confirmed by Rösler, who also showed that in the sparrow, goose, swallow and pee-wit, the primordia of the lungs develop before the primordium of the laryngo-tracheal canal.

These observers did not investigate the forward extension of the larynx into the pharynx.

In a 3·1/2 day embryo of Gallus (figs. 28–31) the tracheo-laryngeal groove extends from 150 μ behind the 4th gill-clefts to a little in front of it. Dense mesenchyme surrounds the oesophagus and tracheo-laryngeal groove.

In a 4 day embryo (figs. 32–35) the anterior-posterior limits of the tracheo-laryngeal groove are the same; the groove is a little deeper in front of the 4th gill-clefts. The primordium of the Constrictor oesophagi and laryngeal muscles is present as a horse-shoe shaped mass arching over the oesophagus and tracheo-laryngeal groove.

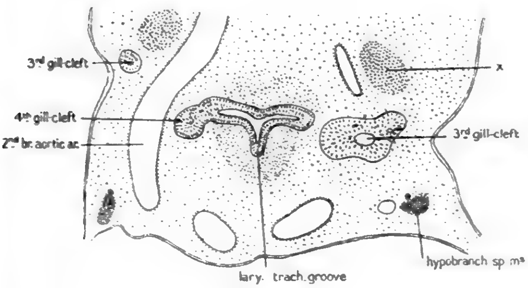

Fig. 32.

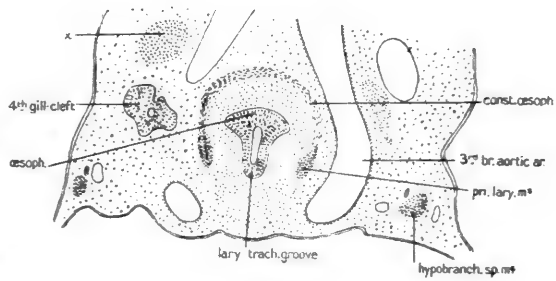

Fig. 33.

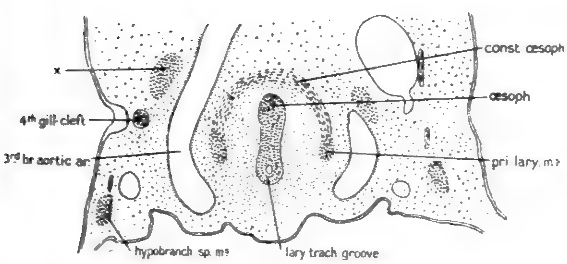

Fig. 34.

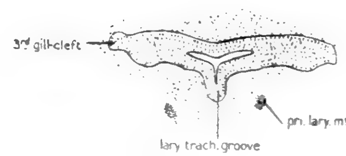

Fig. 36.

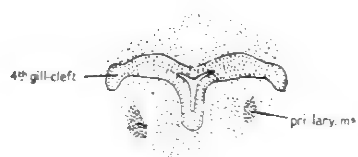

Fig. 37.

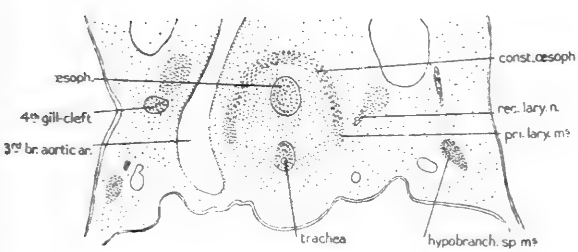

Fig. 35.

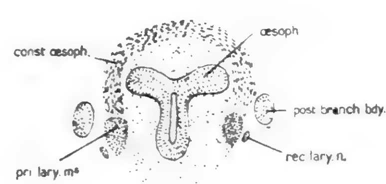

Fig. 38.

In a 5 day embryo (figs. 36–38) the tracheo-laryngeal groove extends from 170 μ behind the 4th gill-clefts to the level of the 3rd gill-clefts. The primordium of the laryngeal muscles has separated, on each side, from the ventral edge of the Constrictor oesophagi; it extends from 140 μ behind the 4th gill-clefts to the level of the 3rd gill-clefts. The recurrent laryngeal nerve lies on its outer side.

In a 6 day embryo (figs. 39–41) the tracheo-laryngeal groove is continuous solely with the pharyngeal epithelium, extending from just in front of the 4th gill-clefts. The lumen of the trachea extends into the ventral part of the larynx. The primordium of the laryngeal muscles extends from 160 μ behind the 4th gill-clefts to the level of the 3rd gill-clefts. In front of the 4th gill-clefts it is broader and thicker than it is behind, and approaches its fellow ventrally.

In a 7 day embryo (figs. 42–44) the primordium of the laryngeal muscles has separated into the (lateral half of) Constrictor laryngis and Dilatator laryngis. The former is obliquely situated and meets its fellow dorsally and ventrally.

In a 10 day embryo (figs. 45–47) the primordia, not yet chondrified, of the cricoid, procricoid, and arytenoid, cartilages are distinguishable in the dense mesenchyme surrounding the larynx.

The above described phenomena in Sauropsida can be summarised as follows. The tracheal and laryngeal epithelium is formed, from behind forwards, as a median groove in the floor of the oesophagus and pharynx. In Chrysemys and Gallus the infolding extends forwards into the last branchial segment—the 3rd branchial in Chrysemys and the 2nd branchial in Gallus. In Tropidonotus, probably in relation with the secondary form of the tongue, it extends into the hyoid segment. The trachea is constricted off from the oesophagus, from behind forwards. In the laryngeal region the walls of the groove come together, and the lumen is afterwards established, in continuity with that of the trachea, from behind forwards. The aditus opens, much later, by separation of the lips of the groove.

The laryngeal musculature, on either side of the tracheal groove, is formed by separation of the ventral edge of the ∩-shaped primordium of the Constrictor oesophagi. It migrates forwards into the branchial s. pharyngeal region. The recurrent laryngeal nerve grows forwards concurrently. The muscle primordium separates, in Chrysemys and Gallus, into the lateral half of the Constrictor laryngis and Dilatator laryngis; in Tropidonotus into the Laryngei and Dilatator.

The laryngeal and tracheal cartilages are developed by chondrification in a thick cellular sheath which develops round the larynx and trachea. In Chrysemys and Gallus the arytenoids become separate structures, in Tropidonotus they remain in continuity with the cricoid.

On the primitive form of the laryngeal muscles in Sauropsida. Göppert stated that in Tropidonotus natrix and Coronella laevis Laryngei dorsalis and ventralis are present, that in Crocodilus biporcatus the Constrictor consists anteriorly and posteriorly of sphincter fibres and in the middle of Laryngei, and that in Midas and Sphargis coriacea whilst the main mass is a sphincter there is anteriorly a Laryngeus ventralis.

He concluded from the above that the primitive form in Reptiles is Laryngei and that a Constrictor is secondary. (He had previously come to the same opinion in Amphibia.)

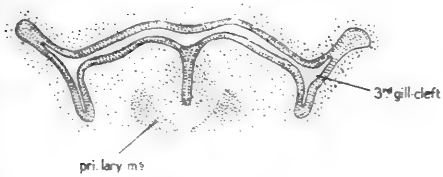

Fig. 39.

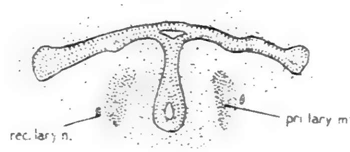

Fig. 40.

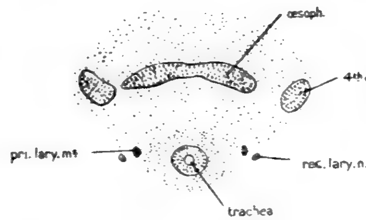

Fig. 41.

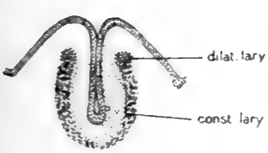

Fig. 42.

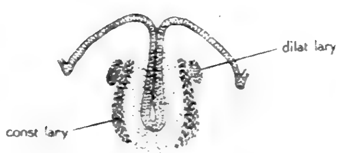

Fig. 43.

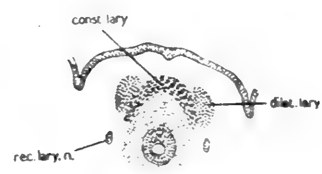

Fig. 44.

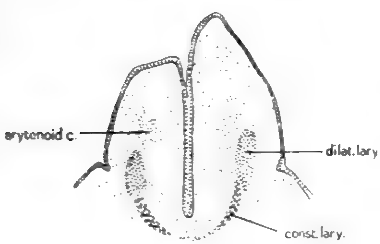

Fig. 45.

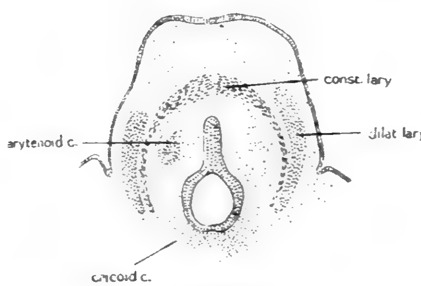

Fig. 46.

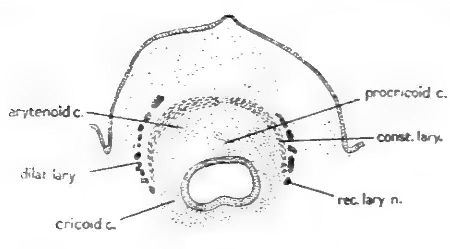

Fig. 47.

This, however, is by no means certain, for in Tropidonotus (vide figs. 24–27) the dorsal musculature is in part a Constrictor, in Chrysemys and Gallus the developmental stages show no trace of the Constrictor being formed by fusion of Laryngei. Hoffman states (in Bronn) that in Reptiles the usual condition is a Constrictor, and Gadow that the condition in Birds is a Constrictor.

These facts suggest that the ancestral Sauropsidan condition was a Dilatator and a Constrictor laryngis.

Some further considerations on the laryngeal muscles are deferred to a later paper.

I have to thank the Bristol University Colston Society for defraying the expense of the above described investigation.

July 11, 1919.

LIST OF FIGURES

The figures are taken from serial transverse sections—in all cases the lowest number denotes the most anterior section.

Chrysemys.

Figs. 1–3 through an embryo 6 mm. long. Fig. 1 through the 5th gill-clefts, figs. 2 and 3 behind them.

Figs. 4–6 through an embryo 7 mm. long. Fig. 4 through the 4th gill-clefts, fig. 5 through the 5th gill-clefts, fig. 6 behind them.

Fig. 7 through an embryo 8 mm. long behind the 5th gill-clefts.

Figs. 8–10 through an embryo 9 mm. long. Fig. 8 through the 4th gill-clefts, fig. 9 through the 5th gill-clefts, fig. 10 behind them.

Figs. 11–14 through an embryo 12 mm. crown-rump length.

Figs. 15–16 through an embryo 15 mm. crown-rump length.

Tropidonotus.

Figs. 17–20 through an embryo, stage (i): fig. 17 through the 4th gill-clefts, fig. 18 through the 5th gill-clefts, figs. 19 and 20 behind them.

Figs. 21–22 through an embryo, stage (ii): fig. 21 through the 2nd gill-clefts, fig. 22 between the 2nd and 3rd gill-clefts.

Figs. 23–27 through an embryo 6 cm long.

Gallus.

Figs. 28–31 through an embryo of 3·1/2 days' incubation; fig. 28 through the 3rd gill-clefts, fig. 29 between the 3rd and 4th gill-clefts, fig. 30 through the 4th gill-clefts, fig. 31 behind them.

Figs. 32–35 through an embryo of 4 days' incubation; fig. 32 through the 4th gill-clefts, figs. 33–35 behind them.

Figs. 36–38 through an embryo of 5 days' incubation; fig. 36 through the 3rd gill-clefts, fig. 37 through the 4th gill-clefts, fig. 38 behind them.

Figs. 39–41 through an embryo of 6 days' incubation; fig. 39 through the 3rd gill-clefts, fig. 40 between the 3rd and 4th gill-clefts, fig. 41 through the 4th gill-clefts.

Figs. 42–44 through an embryo of 7 days' incubation.

Figs. 45–47 through an embryo of 10 days' incubation.

ABBREVIATIONS

arytenoid c.	arytenoid cartilage
br. aortic ar.	branchial aortic arch
const. lary.	constrictor laryngis
const. oesoph.	constrictor oesophagi
c. branchiale i	cornu branchiale i
c. hyale	cornu hyale
cricoid c.	cricoid cartilage
dilat. lary.	dilatator laryngis
dor. aor.	dorsal aorta
hypobr. sp. ms.	primordium of hypobranchial spinal muscles
lary. dors.	laryngeus dorsalis
lary. vent.	laryngeus ventralis
oesoph.	oesophagus
procricoid c.	procricoid cartilage
proc. ant. inf. cric.	processus anterior inferior of cricoid cartilage
proc. ant. sup. cric.	processus anterior superior of cricoid cartilage
procricoid c.	procricoid cartilage
postbranch. bdy.	postbranchial body
pri. lary. ms.	primordium of laryngeal muscles
rec. lary. n.	recurrent laryngeal nerve
sup. lary. br. x.	superior laryngeal branch of vagus
lary. trach. groove	laryngo-tracheal groove
trans. groove	transverse groove
x.	vagus nerve

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PERSISTENT FORAMEN PRIMUM, WITH REMARKS ON THE NATURE AND CLINICAL PHYSIOLOGY OF THE CONDITION

By ALEXANDER BLACKHALL-MORISON, M.D., F.R.C.P.

M. G., 43 years of age, married, and the mother of five healthy children, was admitted on July 15th, 1918, under my care at Mount Vernon Hospital at Northwood. She was stated to have had rheumatic fever when a child seven years old, and for twelve months prior to admission to have suffered from a degree of dyspnoea with palpitation of the heart and some swelling of the feet.

On examination, the apex beat was found to be in the sixth left interspace five inches from mid-sternum in the dorsal position. On right decubitus the apex beat was in the fifth left space three inches from the mid-sternal line. That is, there was no symphysis cordis. The left upper ventricular dulness lying on the back was at the third left rib and the right cardiac dulness at the left edge of the sternum. There was systolic pulsation in the suprasternal fossa and some fulness and pulsation in the right external jugular vein.

There was a systolic bruit of rather high pitch, loudest in a space three inches from mid-sternum to the apex beat. It was traceable to the left and distinctly audible in the left paravertebral groove and also, but less so, in the right paravertebral groove. The aortic valves were heard to close perfectly in diastole and there was no reduplication of the second sound of the heart. The closure of the pulmonary arterial valves was palpable. While, therefore, I had some doubt as to the precise character of the lesion, I was inclined to regard it as one permitting reflux through the mitral valve. I think I was justified in doing so, for reasons which I need not detail here, but I was, nevertheless, wrong, as the conditions found after death proved. The pulse rate at this period was 84 to 96 and its rhythm regular.

Examined later, the physical signs remained much the same, but the area of cardiac dulness was increased, and the pulse rate was accelerated and it had become irregular. The patient had, at this period, a long sustained attack of paroxysmal tachycardia, when the pulse rate reached 198 in the minute. There was passive congestion of both lungs and enlargement of the liver with signs of commencing stasis in the systemic venous system. From this grave condition the patient partially recovered; the paroxysmal tachycardia subsided, the pulse rate falling to 92–112; she was able to leave her bed and to sit on a reclining chair and expressed herself as feeling better. But the heart

had entered on the last phase of progressive failure. There was increasing evidence of anasarca, of effusion into the serous cavities in chest and abdomen, and of albuminuria. She became ever more restless and sleepless and finally died collapsed and comatose on Oct. 15th, 1918.

The post-mortem examination was made by Dr Kinton, Resident Superintendent of the Hospital, assisted by Dr R. J. Cyriax, the House Physician. The heart after removal from the body was placed in weak formalin solution for examination later by myself, and I am indebted to Dr Cyriax for the drawing of the conditions found, which I now exhibit.

The general data discovered, bearing upon the condition of the heart, which need be mentioned were, that there was serous effusion into the pleurae and peritoneal cavity and that the pericardial sac contained three ounces of fluid instead of the normal drachm or two; the liver was enlarged, weighing 61 ounces, and showed the usual passive congestion of progressive cardiac failure, as did the lungs and the kidneys. The latter weighed six and five ounces respectively and their capsules stripped off easily. The spleen weighed six ounces.

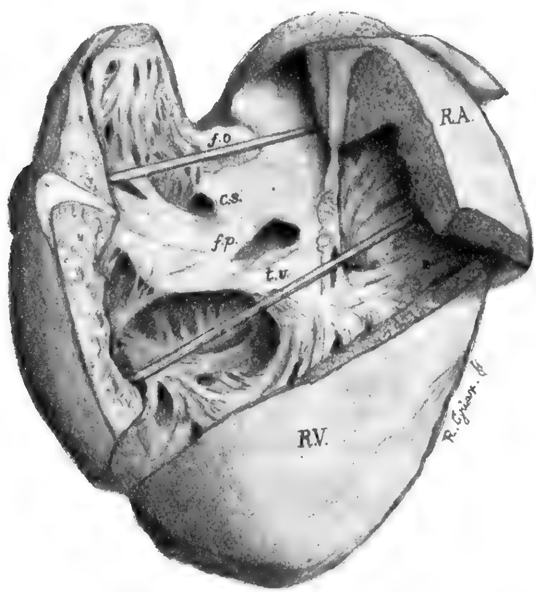
The condition of the heart is as follows: It weighs after evacuation of blood and hardening in formalin solution, one pound seven ounces, that is, it has at least twice the average weight of the normal female heart. On the anterior surface of the left ventricle, near its apex, there is a milk spot measuring 2·5 by 3 cms.

The right auricle is markedly hypertrophied. The auricular wall near the auriculo-ventricular junction measures 1·5 cms., that is, about half an inch. The musculi pectinati, crista terminalis and other muscular markings are well defined. The foramen ovale is large and completely closed. The entrances of the inferior and superior venae cavae are normal and the muscular anterior wall of the superior caval entrance powerfully hypertrophied. The orifice of the *coronary sinus* is rather smaller than usual.

Below and anterior to the coronary sinus and immediately above the insertion of the septal cusp of the tricuspid valve there is *an orifice* large enough to admit the forefinger and passing directly into the left auricle. The attachment of the septal cusp partly by very short cordae tendinnae and chiefly by direct adhesion to the moderator band in the right ventricle is extremely short and tight. It could have exercised little valvular function. The anterior cusp appears to be normal and the posterior rather smaller than usual. The atrio-ventricular orifice admitted three fingers and from its anatomical condition probably permitted regurgitation into the auricle. All measurements it will be noted are after immersion in formalin solution and, therefore, are probably smaller than in life.

The *right ventricle* is powerfully hypertrophied, its wall having a diameter of 2 cms. near the auriculo-ventricular junction and of 1·5 cms. about the middle of the chamber. The *moderator band* is well developed and the columnae carneae and trabeculae generally, powerfully hypertrophied. The valves of

the pulmonary artery are normal, competent and rather capacious. The pulmonary artery itself is dilated and its wall thicker than usual but there is no atheroma. The *left auricle* is normal and in no way hypertrophied. The left auriculo-ventricular orifice admits two fingers from above. The finger passed through the persistent foramen primum, goes directly into the left atrio-ventricular orifice. The left ventricle although well developed muscularly is not markedly hypertrophied. Its walls measure at thickest 2 cms., the cavity is not dilated and the papillary muscles and trabeculae generally are not hypertrophied. The *mitral cusps* are well formed and apparently competent. The *aorta* is practically free from atheroma, rather below the average



Persistent Foramen Primum showing interior of right auricle and ventricle. The walls are held apart by glass rods. ½ nat. size. *R.A.* right auricle; *f.o.* foramen ovale; *c.s.* coronary sinus; *f.p.* foramen primum; *t.v.* tricuspid valve; *R.V.* right ventricle.

in size and its walls are thin. The three semilunar cusps are normal and the posterior one attached to a deep sinus of Valsalva. There are two patent coronary arteries. The interventricular septum is perfect.

Remarks. As the interauricular curtain (septum primum) is dropped, in embryo, towards the endothelial cushions which mark the line of the auriculo-ventricular valves, in certain cases, the growth of the septum is arrested and a communication between the auricles remains, which under normal circumstances would not be present. A section of the arrested curtain, examined microscopically, shows it to be a true arrest of development and not the result of any foetal endocarditis (Morison, *Journ. of Anat. and Phys.* vol. XLVII. p. 467).

This communication may be large or small. In a case which I showed before this Society in 1913 (*Journ. of Anat. and Phys. loc. cit.*) it was very large and incompatible with any length of life. The child, a male, died when six months old, after having been under observation for one month. It showed after death, collapsed lung with scattered patches of induration, which were probably atelectatic, although they were not examined microscopically—a persistent foetal state. There was hypertrophy of the right auricle and ventricle, none of the left auricle and little of the left ventricle and, as in the present instance, a small coronary sinal orifice. The bruit observed clinically was also systolic and apical but heard best in the back.

Professor Keith remarks, in his lectures on Malformations of the Heart (*Lancet*, vol. II. 1909, p. 435) that this defect "is not necessarily accompanied by grave disturbance of the heart." The defect is, however, very apt to be associated with some abnormality of the auriculo-ventricular valves as is readily conceivable from the position and nature of the defect. Dr Maude Abbot (*Osler and McCrea's System of Med.* vol. IV. p. 357, 2nd edition) relates that, in five out of seven cases reported by Rokitansky, the anterior segment of the mitral valve was "cleft from its free border to its insertion." In the case which I now show the mitral valve was normal but the septal cusp of the tricuspid valve was, as I have stated, adherent to the moderator band so as to be functionally incompetent.

Although, as in the present case, the bearer of the lesion may live for a considerable period and fulfil the ordinary functions of the human being—in this case the cardiopath as stated had five children and was 43 years of age—I do not know whether any of the cases presenting this defect have been much older. If they have, it will probably be found that the defect had developed in such a manner as to leave the atrio-ventricular orifices well guarded by their valves.

In 1918, I showed before the Society the heart of a man with a much stenosed pulmonary arterial orifice, a shrunk right ventricle and a hypertrophied and dilated right auricle. The owner of it died at the age of 72, but in this case, the avenue of relief between the auricles was a largely patent foramen ovale, the septa of the auricles and ventricles being otherwise normally complete. But patency of both the foramen ovale and foramen primum may co-exist (Thomson, *Proc. Anat. Soc.* 1902–3, XXXVI.). The case I now show (Mrs G.'s) also illustrates the secondary pathological changes usually observed in persistent foramen primum, namely, general escape of the left chambers from hypertrophy, some hypoplasia of the aorta, dilatation of the pulmonary artery, marked hypertrophy of the right chambers and, as I have pointed out, a certain smallness of the orifice of the coronary sinus.

To a clinician, all such conditions, primary and secondary, are of interest, as indicating where the strain of conducting the circulation has been most felt by the heart. As these points are a matter of morbid physiology they may be mentioned here. I should myself feel disposed to modify the conclusion

expressed by Professor Keith already quoted, by maintaining that the defect "is not necessarily accompanied by grave disturbance of the heart," but only for a time, and that it always ultimately causes grave disturbance and is incompatible with length of life in proportion to the degree in which the atrio-ventricular valvular apparatus is involved in the genesis of the defect.

Clinically the rhythm and situation of the bruit audible in these cases is of interest. In both my cases the bruit was systolic in time, mainly apical in situation and audible (unlike the presystolic bruit of mitral stenosis) posteriorly as well as anteriorly. Without atrio-ventricular valvular defect or incompetency, one would expect any bruit present in persistent *foramen primum* to be presystolic, that is, auricular systolic in time. But if this time of the bruit be observed in such a case, it will probably be found as I have stated, that it is audible posteriorly as well as anteriorly. It is very desirable in all cases of congenital heart disease, if any bruit be present, that it should be very carefully noted as to character, rhythm and localisation, for diagnostic purposes.

It is evident from what has been said as to the condition of the chambers in the left or arterial heart that the strain of the circulation in these cases is chiefly upon the dextral chambers.

The hypoplasia of the aorta, taken in connection with the dilatation of the pulmonary artery, in the absence of left auricular dilatation and hypertrophy, together with the lack or small degree of hypertrophy of the left ventricle, points to a deficiency in the normal plenitude and permeability of the pulmonary circulation. This is probably due in a measure to a persistence of the foetal condition, in so far as the defect diminishes the aspirative and propulsive force of respiration. In the completely foetal condition, the extent of the pulmonary circulation being at a minimum and the transmission of the blood to the arterial system secured by adequate channels, no dilatation of the pulmonary artery occurs, but the right chambers preponderate in power and in muscular development over the left.

In persistent foramen primum, on the other hand, extra uterum, the lungs are in action, and a large quantity of blood *does* reach the pulmonary circulation but without the full aid of the aspirative force resident in the normally constituted left heart. With the closure or the practical closure of the ductus arteriosus under these circumstances, the powerful right ventricle, while it fails to drive sufficient blood through the lungs into the left heart, tends, in diastole, to retain blood in the pulmonary artery and its main branches. Hence their dilatation and the baggy valves which guard that vessel. The incomplete plenitude of left cardiac blood thus serves to explain the total absence of left auricular and the comparative absence of left ventricular hypertrophy in these cases and likewise the hypoplasia of the thin walled aorta met with in many such instances. That very considerable hypertrophy of some parts of the organ is, nevertheless, present is proved by the notable increase in the weight of the organ and this, in the absence of vascular or renal

conditions, is calculated to induce hypertrophy of the cardiac muscle from other causes than the purely mechanical cardiac defect.

Finally, it may be stated that the bearer of the congenital defects (foramen primum and abnormal tricuspid valve) in the present instance, although stated to have suffered from rheumatic fever as a child, showed no evidence in endocardium or pericardium of consequences of that disease. The changes, therefore, noted in the organ were a result of the congenital anatomical states described and the modified physiological actions which resulted from them. Here again, then, as in other cases I have shown to this Society, the importance of integrity of the valvular apparatus, for an efficient and easy conduct of the circulation through the heart, is manifest.

In Memoriam

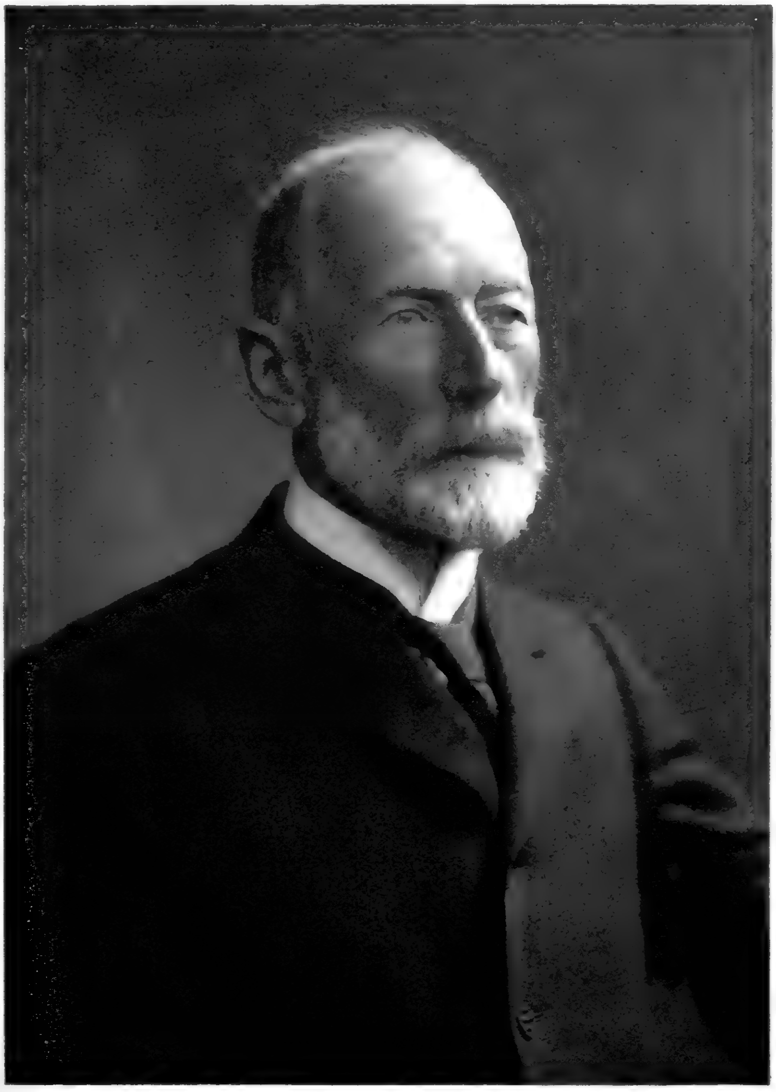
PROFESSOR ALEXANDER MACALISTER, M.D., F.R.S., ETC.
1844—1919

ONE of the earliest and strongest links in the history of the *Journal of Anatomy* and of the Anatomical Society has been broken by the deeply lamented death of ALEXANDER MACALISTER.

Ever active in promoting the interests of the *Journal* his name is appended to an interesting paper on muscular anomalies appearing in the first volume and its earlier pages are rich in his learned and thoughtful contributions. In 1898 he joined the editorial staff becoming acting editor in 1910. As acting editor he was indefatigable, reading every paper submitted to him with the most scrupulous and meticulous care and earning the gratitude of many a contributor for advice, information and help. He was always of the opinion that the *Journal* should be well illustrated and spared no trouble and expense to this end.

The Anatomical Society must regard Macalister as one of its parents. It was initiated in 1887 as the result of a series of week-end conferences held at Cambridge in 1886 between Humphry, Lockwood and himself. For years he was a constant attendant at its meetings, took an active part in its proceedings, and was its President in 1898. In 1889 he drew the attention of the Society to the desirability of a scheme for coordinated research. The resulting Committee of Collective Investigation accumulated a considerable amount of valuable information but came to an untimely end. He always held the view that the *Journal* should be under the direct management of the Society and it was largely due to his warm advocacy and unselfish interest that this was brought about last year.

The story of Macalister's early life reads more like a romance than sober fact. He was born in 1844 in Dublin, whither his father, Robert Macalister of Paisley, had migrated to succeed Will Carleton, the Irish novelist, as Secretary to the Sunday School Society of Ireland. Robert Macalister, blessed with a large family and a slender purse, destined his son Alexander to a business calling. As a school-boy he developed the most diligent habits and early displayed a love for biological study spending all his available leisure time in the Glasnevin Botanic Gardens. There he attracted the attention and interest of the Curator who recognising that he was no ordinary boy persuaded his father to let him study Science. Consequent on special recommendation



Phot. by Lafayette

PROFESSOR ALEXANDER MACALISTER,

M.A., M.D., LL.D., D.Sc., F.S.A., F.R.S.

he was allowed to commence his medical studies at the Royal College of Surgeons of Ireland at the incredibly early age of 14. From this point his progress was meteoric. He was appointed Demonstrator of Anatomy at the College at 16 and at 17 obtained the double qualification. Entering Trinity College Dublin, he was elected Professor of Zoology at the University of Dublin while still an undergraduate, and was precluded from proceeding to an honours degree in Science, the would-be examinee being an examiner. Could anyone imagine a more Gilbertian situation? In addition to his professorial duties he lectured on Botany, Geology, Astronomy and I know not how many other sciences at Alexandra College, Dublin. In 1877 he was appointed Professor of Anatomy and Chirurgery at Trinity College, Dublin and Surgeon to Sir Patrick Dun's Hospital. Six years later he succeeded Humphry in the Chair of Anatomy at Cambridge, where he laboured incessantly and with the utmost devotion for 36 years, for the same length of time as Turner held the corresponding chair at Edinburgh.

In his early years Macalister was a most prolific writer—text-books, monographs and papers following one another with startling rapidity. Special attention may be recalled to his "Observations of Muscular Anomalies," read in abstract before the Royal Irish Academy in January 1871, and compiled during a Summer recess in the previous year. A complete survey of the variations affecting the whole muscular system of man it was a most amazing piece of work and a wonderful tribute to his immense patience and untiring energy. Careful study reveals the fact that not only did he collate everything that had ever been written on the subject but 50 per cent. or more of the material which he presents is the result of his own personal observations —observations which having stood the test of years and been confirmed again and again have become classical. He confesses to having taken part in the dissection of over 690 subjects, while the tedious and intricate dissections necessary to furnish him with such numerous examples from the face, scalp, pharynx, soft palate, etc. transcend the imagination. This is the work of a young man of 26, immersed in professorial duties and busily engaged in laying the foundations of two large treatises on Zoology to appear a year or two later.

His great text-book of Anatomy, great in more senses than one, was published in 1889. There are few anatomists but owe a debt and that a considerable one to its pages. Utterly unlike anything that has appeared before or since it was no mere compilation but original in thought and treatment, replete with personal observation and an index of the man himself. If fault it had it was that of compression. Macalister had so much to tell and the confines of a large text-book were for him so limited that he was forced to prune, curtail and abbreviate at every step. The wonder is that no second edition ever appeared but therein lies a tragedy. An interleaved copy of the book was always lying on his table and in this he daily added new facts, observations and reflections until in a few years time it was full to overflowing. One day it disappeared never to be found again. Its loss was met with characteris-

tic and cheerful fortitude, but it was a blow from which he never recovered, and it sealed the fate of a subsequent edition.

Macalister was wont to give a course of lectures on the historical aspects of Anatomy in the Summer term at Cambridge. Choosing a new subject year by year he covered a vast field, giving his critical acumen full play, displaying a wonderful power of broad survey and discovering links hitherto unsuspected. Most especially is it to be regretted that he never fulfilled the hope expressed in the preface of his text-book to write a "detailed history of the progress of Anatomical discovery." No one in the world was better equipped for the task. Exploring anatomical literature had long become a habit and he had spent much of his life in the University Library at Cambridge, rich beyond compare in the works of the earlier anatomists. He gives us some foretastes of what might have been in his "Memoir of James Macartney," "A Sketch of the History of Anatomy in Ireland," "The History of the Study of Anatomy in Cambridge" and "Archaeologia Anatomica" which appeared from time to time in the *Journal of Anatomy*, and which though unsigned were the products of his pen.

The eminent service Macalister rendered in elevating Anatomy from a mechanical study into a living science is perhaps insufficiently realised at the present day. No bare fact ever presented itself to him but it set him thinking of the part it played in the mystery of life and the problem of existence. This may not be apparent in many of his writings, but was pre-eminently so in his teaching and influence. An exception to this general statement is afforded by "Some Morphological Lessons taught by Human Variations," a Robert Boyle lecture delivered at Oxford in 1894. Therein he sets forth in masterly fashion the deductions he draws from a study of variations to the garnering of which he had always been irresistibly attracted.

Endowed with a marvellous and orderly memory, infallible and almost uncanny in its tenacity for minute detail, Macalister had the most astounding facility for accumulating information and facts not only from books but at first hand from dissecting room and museum. He would devote endless pains and infinite patience to obtaining and noting new facts, but once acquired they seemed to lose further interest and he could rarely be prevailed upon to publish them. Not a tithe of them appear in his published writings, some lie stored in countless note-books, but many alas! are gone with him. In the disposal of his stores he was generosity itself, they were offered freely and openly to one and all to make what use of them they liked.

His lectures were an intellectual treat and are held as most valued recollections by all who were privileged to listen to them. His facile eloquence, lightened by occasional flashes of quaint dry humour, would at times fascinate and almost mesmerise his hearers. Following no tradition, shackled by no exigencies of examination, a rich spring of anatomical knowledge, ornate with morphological illustration and historical interlude, flowed out in a quiet but inspiring stream.

No professor ever spent so many hours in the dissecting room. He revelled in the practice of his art and was the neatest and most rapid exponent I have ever seen, devoting the same scrupulous care to the most trivial display as to the most intricate manipulation.

To do adequate justice to Macalister's great learning and scholarship is an impossible task. Although he knew more about the anatomy of the human body than any man living, anatomy after all was but a small part of his mental equipment. He was an able mathematician and familiar with many languages both living and dead. In Archaeology, Zoology, Egyptology, Theology, Biblical history, to mention but some of the subjects which aroused his interest, he was an inexhaustible mine of knowledge. In discussion on many and diverse subjects, he was conspicuously the authority and source of accurate information, often to the confusion of the expert. His indefatigable industry and insatiable thirst for knowledge persisted throughout life and in these respects he never grew old.

Despite his great attainments he had the most kindly and gentle disposition, was ever considerate for the opinions and feelings of others and endeared himself to all who met him. It was an inestimable privilege to have known him and his loss leaves a blank which can never be filled.

E. B.-S.

REVIEWS

THE PERIPHERAL NERVES

THE aid of the anatomist—in many places his personal aid—has been much sought by the surgeon in the extensive and detailed knowledge of the peripheral nervous system which has been demanded of him during recent years. It is with considerable interest, therefore, though mingled with a sense of the personal loss, that one turns to the volume on this subject by the late Professor Paterson[1], knowing that it has been written by an anatomist of authority and by one with the experience of the R.A.M.C. officer. His book is founded, even at first sight, on a wide basis, since by an appeal to the general morphology and development of nerves he has aimed primarily at an explanation of the principles which govern the facts of peripheral nerve distribution. One may doubt the value of, or even disagree with the views expressed in, for example, the chapter on "The Nature of the Limbs," but that Professor Paterson was correct in adopting the broader plan will be felt at once, even by those who may be introduced for the first time to morphological concepts, not merely from the educative point of view, but, for instance, as affording the only assistance towards understanding the "plan" of the common variations of nerves which otherwise remain a seemingly uncalled-for mystery. He has incorporated in his general account of the nerves, in a way which will be recognised as peculiarly his own, many of his own deductions on the critical questions of the subject, and the trained observer is well seen in his notes on the vascularity of the ends of the severed nerves. The book does not aim at being encyclopaedic nor claim to be a book of reference, but as a general statement of the anatomy of the peripheral nervous system by a recognised authority on that subject, it is indeed worthy of the study of those whose work requires the knowledge it contains, and whose inclinations lead them to seek more than the mere summation of fact. The anatomist will pay it the attention it merits from his regard for the writer.

The other book before us on this subject—Dr Whittaker's revisal of the late Professor Hughes' *Handbook of the Nerves of the Body*[2]—is a concise summary of the main facts of the distribution of the peripheral nerves and the sympathetic system, and should serve excellently as a preliminary statement for one revising the empiricism of these subjects. It is, however, the pure hard fact of systematic anatomy, and, though not detracting from its usefulness on that account, is essentially a summarised extract of any good anatomy text-book. The plates are purely diagrammatic, and as such are of assistance to the text. They are well reproduced.

[1] *The Anatomy of the Peripheral Nerves.* Prof. A. M. Paterson, M.D., F.R.C.S. Henry Frowde and Messrs Hodder and Stoughton. pp. vi + 165. 12*s.* 6*d.* net.

[2] *Nerves of the Human Body.* C. R. Whittaker, F.R.C.S. (Ed.) E. and S. Livingstone, Edinburgh. pp. viii + 72. 12 plates. 3*s.* 6*d.* net.

STUDIES ON THE ANATOMICAL CHANGES WHICH ACCOMPANY CERTAIN GROWTH-DISORDERS OF THE HUMAN BODY

By ARTHUR KEITH,

Royal College of Surgeons of England

I

THE NATURE OF THE STRUCTURAL ALTERATIONS IN THE DISORDER KNOWN AS MULTIPLE EXOSTOSES[1]

During the last ten years I have paid particular attention to the structural alterations which occur in men and women who are, or have been, the subjects of disease of one or more of the glands of internal secretion[2]. In several instances I have to admit, that the relationship between the structural alterations and a disorder of the glands of internal secretion is highly problematical; in many cases, however, such as acromegaly, giantism, precocity of sexual development and cretinism, we must admit that there is a direct connection between a disordered action of the endocrine glands and the appearance of a crop of structural changes. My aim in studying these disorders has been to gain a more accurate knowledge of the mechanism of normal growth—for a knowledge of the conditions which determine the shape and size of the various structures of the animal body must always have a prime importance for anatomists. In her aberrations, as I shall attempt to show, Nature often uncovers parts of her very elaborate growth machinery.

The disorder which I am to deal with first—multiple exostoses—is usually placed by surgeons in the category of tumours, but a close examination of its anatomical changes shows that it should be definitely placed among the disorders of growth and given a name to indicate its true nature. The name I propose, one suggested to me by Mr Morley Roberts, is *Diaphysial aclasis*, because the main incidence of the disturbance falls upon the modelling or pruning of the diaphyses or shafts of bones. My attention was drawn to the nature of this disorder in the following way. In the summer of 1918 Capt. J. A. Annan sent to the War Office Collection at the Royal College of Surgeons a series of X-ray plates he had taken of a young man, aged 20, serving as a private in a labour battalion in France. This man had been admitted to the 3rd Canadian General Hospital where he was recognised as a subject of

[1] The publication of this Research has been defrayed by a grant from the Medical Research Council.

[2] "An Enquiry into the Nature of the Skeletal Changes in Acromegaly." *Lancet*, 1911, I. p. 993. "Abnormal crania, Achondroplastic and Acrocephalic." *Journ. of Anat. and Physiology*, 1913, vol. XLVII. p. 189. "Progeria and Ateleiosis." *Lancet*, 1913, I. p. 305.

multiple exostoses. The bony tumours situated in the neighbourhood of the knee and ankle, unfitted him for active duties and he was discharged from the army. My attention was arrested by the skiagraphs taken from his knee joints. An exact drawing is given of the appearance of the lower end of the left femur and upper end of the left tibia in Fig. 1. The lower femoral epiphysis is normal in size and outline, but the lower end of the femoral shaft is represented by a cylindrical mass of irregularly formed bone, showing

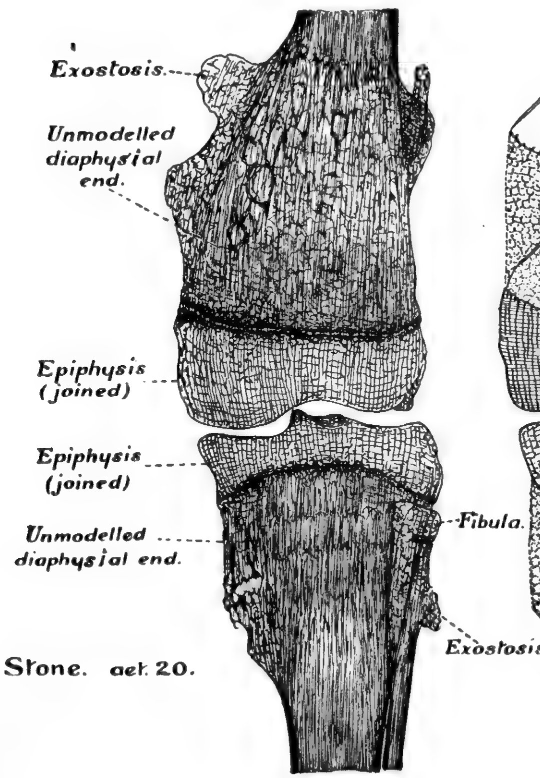


Fig 1.

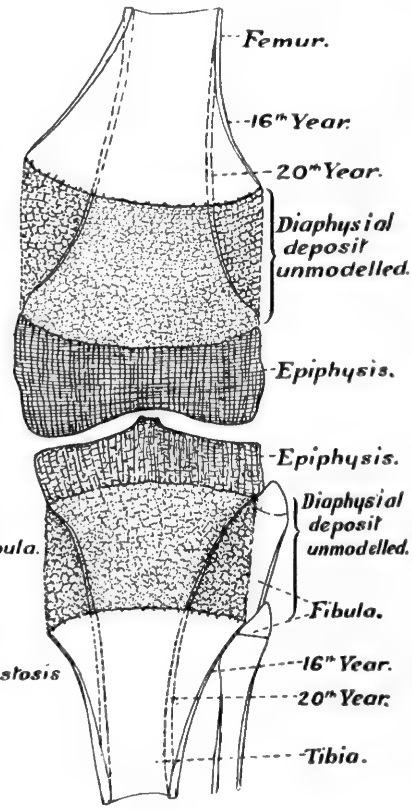


Fig 2.

Fig. 1. Drawing from a skiagraph of the region of the left knee of a man aged 20, the subject of multiple exostoses (½ nat. size).

Fig. 2. Drawing to illustrate Hunter's modelling process.

a gravely disturbed architecture. The irregular mass of bone represents the growth of several previous years. The cylindrical medullary shaft instead of reaching almost to the epiphysis is separated from it by an irregular column 90 mm. long by 75 mm. wide as measured on the skiagraph. Similarly between the modelled shaft of the tibia and its upper or proximal epiphysis is interposed an ill-formed cylinder, 60 mm. long by 80 mm. wide. The right knee showed a corresponding disorder of growth. In both right and left limbs the femoral

and tibial diaphyses had commenced to unite with their corresponding epiphyses. Further enquiry showed that there were similar disturbances at the lower ends of the tibia and fibula, at the upper end of the femur, at the distal ends of the radius and ulna, at the proximal end of the humerus, while at the elbow joint there were certain irregularities which will be noted further on. A reference to Fig. 2 will serve to explain my interest in the irregular bone development shown in Fig. 1. One of John Hunter's more important discoveries was his realisation that the shafts of bones grew in length by a double process; there was first the deposition of new bone in the cartilaginous growth disc at the ends of the shaft, a process clearly recognised before Hunter's time; there was in the second place a "modelling process" by which the new bone thus laid down was pruned, reformed and incorporated as an intrinsic architectural part of the cylindrical shaft. Hunter clearly recognised that these two processes were independent operations. If Hunter's teaching is true then we ought to find disorders of growth in which deposition of new bone goes on while the second or remodelling process is retarded or even completely arrested. A survey of the skiagraphs of the first case of multiple exostoses that came my way showed me that in this disorder the deposition process goes on but the modelling process is retarded and aberrant. In multiple exostoses, which is a disorder of youth and of adolescence, then, the modelling process is profoundly retarded; in some instances almost arrested. The bony excrescences or tumours, which serve as diagnostic marks for the clinical recognition of the condition, are merely secondary results of the primary disorder of growth for which I propose the name of *Diaphysial aclasis*.

For a complete set of skiagraphs of a second case I have to thank my friend Capt. Lionel West. He sent to me, for the War Office Collection, full records of a man aged 26 he had under his observation in the Military Hospital at Prees Heath. In neither this case, nor the last, was a full family history obtainable, not for lack of enquiry but because neither man had a very full knowledge of his relatives. Capt. West's case was in every way similar to Capt. Annan's, except that the epiphyses had completely united with the shafts and there was a more definite arrangement of the cancellous trabeculae in the direction of the lines of force. In Capt. West's case, the man's stature was five feet (1524 mm.); in Capt. Annan's case the exact height was not taken but he was undersized. For a third case, also added to the War Office Collection, I am indebted to Dr Florence Stoney. In this case the man was aged 29 and the modelling process had been much less retarded than in the two younger men. In Dr Stoney's case a brother and four maternal uncles were affected with the same disorder. A survey of recorded cases shows that about half the subjects have one or more relatives similarly affected, and that the disorder is Mendelian in its incidence. The skiagraphs of a fourth and very instructive case were placed at my disposal by Mr W. Rowley Bristow of St Thomas's Hospital. One set of plates were taken in February, 1919, a second set, exposed exactly as the first set had been, were taken in December

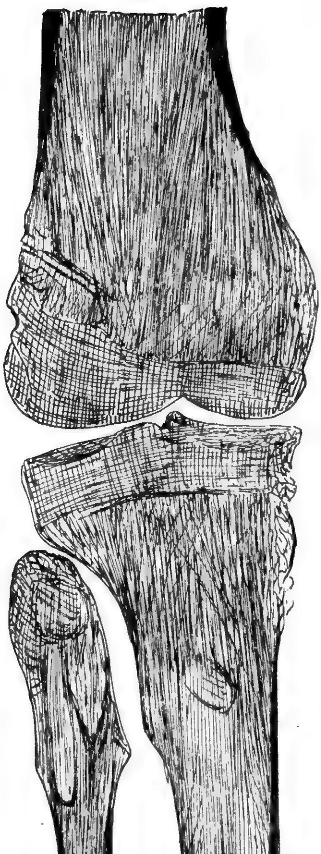


Fig 3.

Mather. aet. 29.

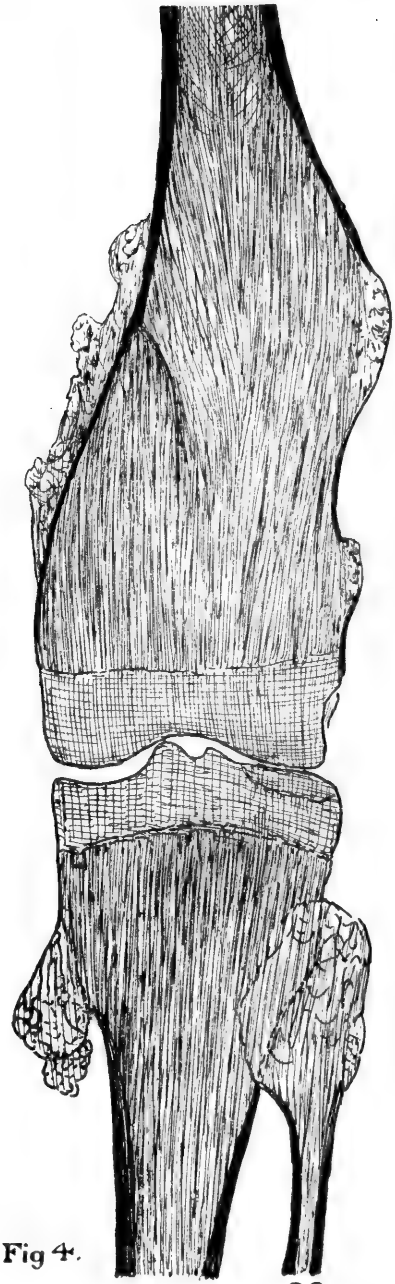


Fig 4.

Gregory. aet. 26.

Fig. 3. Skiagraph of the right knee of Dr Florence Stoney's case. The arrest of modelling is much slighter in degree than in Capt. Lionel West's case (Fig. 4). In the latter case two areas of exostosis are seen on the lateral aspect of the femoral shaft; between these areas periosteal bone is being deposited. An exostosis also grows from the medial aspect of the proximal end of the tibia. In both cases the proximal end of the fibula is thickened and ill formed; in Fig. 4 there is ossific union between the proximal ends of the shafts of the tibia and fibula.

of the same year. The subject of the disease was a girl aged 16; by the superimposition of tracings from these two sets of plates I was able to determine accurately the growth changes which had occurred in all the long bones of this case in the preceding ten months. Mr Laming Evans was also good enough

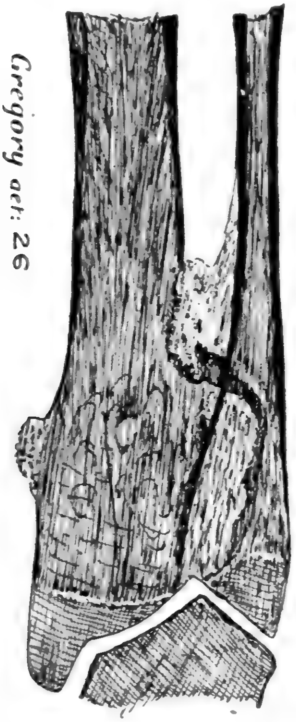


Fig 5.

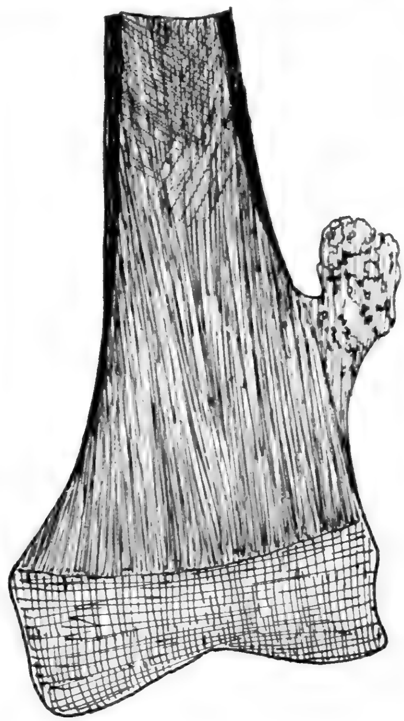


Fig 6.

Fig. 5. The skiagraphic appearance of the distal ends of the left tibia and fibula of Capt. West's case. It will be observed that the lateral border of the trochlear surface of the astragalus has been pushed between the epiphysial ends of the leg bones. The epiphyses, although clearly differentiated from the shafts, are firmly united with them. There is a mutual interlocking between the outgrowths from the shafts of the tibia and fibula but no ossific union between them. In the right limb the distal ends of the tibial and fibular shafts had grown together and fused.

Fig. 6. Skiagraph of the distal end of a left femur showing a single cartilaginous capped exostosis. There is no arrest of the modelling process. Single tumours or even several cartilage capped exostoses are not necessarily symptomatic of the condition here named Diaphysial aclasis.

to give me access to records and skiagraphs he had made from four cases which he has under observation, and of which he is to publish an account. Two of his cases were particularly useful to me as they represented earlier stages than the four I have enumerated above. Although the disorder is by no means

rare, it is represented very sparsely in the medical museums of London. The only skeletal representation is in the Museum of St Thomas's Hospital where there are preserved the limb bones of a subject of this disease. The dimensions of the bones show that he was a man of small stature and their state, that he was probably over 30 years of age. He committed suicide by throwing himself in front of a railway train, and no family history was obtainable. I am

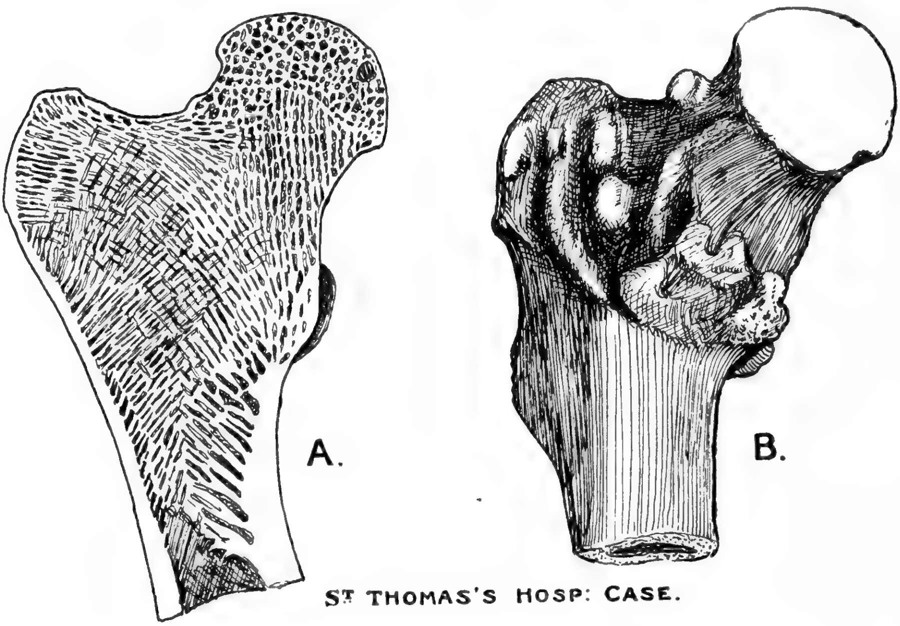


Fig 7. Fig 8.

Fig. 7. Vertical section of the proximal end of the right femur of the case preserved in the museum of St Thomas's Hospital. It will be seen that there has been an arrest of the modelling process shown by the vertical depth of the neck, the low position of the trochanter minor and the imperfect differentiation of the trabecular architecture.

Fig. 8. Exostoses on the outer aspect of the neck of the right femur.

indebted to my colleague Prof. Shattock for an opportunity of making a full examination of the bones of this man. In recent medical literature records can be found of about 300 cases[1], but a survey of a selection of this literature only served to show that the disorder is one which is remarkably uniform and

[1] Some of the more recent records are the following:

McKail, J. *Archives Radiology and Electro-therapeutics*, 1917, vol. XXI. p. 286.

Cowie, Dr David Murray. *Archives of Pediatrics*, 1917, vol. XXXIV. p. 461.

Hess, Dr Alfred F. *Ibid.* p. 462.

Carman, R. D., and Fisher, A. O. *Annals of Surgery*, 1915, p. 142.

Nasse, D. "Ueber multiple cartilaginäre Exostosen und multiple Enchondromata." *Berlin. Sam. Klin. Vorträge Chirurgie*, N.F. No. 124, 1895, p. 209.

Bessel-Hagen, Prof. Fritz. "Ueber Knochen- und Gelenkanomalien." Langenbeek's *Archiv f. Klin. Chir.* 1891, vol. XLI. p. 749.

characteristic and that the material I had in hand was sufficient to exemplify all its predominant features.

We obtain some light on the nature of the disease named Diaphysial aclasis when we note its distribution in the skeleton. All bones which are formed entirely within cartilage are free from any disorder of growth. The tarsal and carpal bones, the epiphyses of all the long bones, the vertebral bodies and sternum are formed in aclastic individuals as in normal persons. So are the bones formed in membrane—the bones of the cranial vault and of the face. In the cases I have seen the facial bones are not robustly modelled—there is a lack of supra orbital ridges and the nose is short and pinched—but there is no noticeable departure from the normal in their development. The disease is confined to those elements of the skeleton where bone laid down within cartilage comes to be covered by periosteal bone as in the shafts of long bones. Hence this disorder of growth falls on the growing ends of the shafts of long bones, where a core of bone formed within cartilage comes to be encased in a sheath of bone formed beneath the periosteum. Where growth is most extensive and most prolonged as at the distal and proximal ends of the femur, tibia and fibula, at the distal ends of the forearm bones and proximal end of the humerus, the aclastic condition is most marked. It is also particularly well seen at the growth line along the vertebral border of the scapula and along the cristal border of the ilium. The outer and inner ends of the clavicle being formed from both cartilage and membrane bone also show an unmodelled formation.

In Fig. 9 there is represented a vertical section of the femur of a turtle to show the relationship of the membrane or periosteal-formed bone to that laid down in cartilage. We have here a diagrammatic representation of the condition out of which the long bones of mammals have been evolved. The cartilaginous extremities are devoid of separate epiphysial formations; there can be no question of an epiphysial line of ossification—only of a diaphysial line at which the shaft increases in length (growth line in Fig. 9). This is also true of mammalian long bones; the growth line has nothing to do with the enlargement of the epiphysis, only of the shaft, and should therefore be called the *diaphysial line*. Now the diaphysial line is made up of two distinct parts, but hitherto we have fixed our attention on only one of these parts—the cartilaginous part of the line in which endochondral bone is laid down. We have omitted to note that the cartilaginous growth disc is surrounded by a periosteal ring or ferrule where growth in length also takes place. The periosteal growth ring represents the margin at which the covering of periosteal bone extends itself over the growing core of cartilage-formed bone. In normal development the cartilaginous core and periosteal proceed at an equal pace. In achondroplasia, the arrest of growth falls on the cartilaginous core; the periosteal ferrule outstrips and overlaps the cartilage-formed bone. In Diaphysial aclasis the opposite is the case; the periosteal extension is arrested and thus areas of cartilage-formed bone are exposed on the surface of the

shaft. The periosteum and the osteoblasts derived from the periosteum are the main agents in the modelling of bone. Hence with the arrest of the periosteal growth ring, the process of modelling becomes retarded and irregular; the diaphysial cartilage thus exposed on the surface is free to expand in abnormal directions.

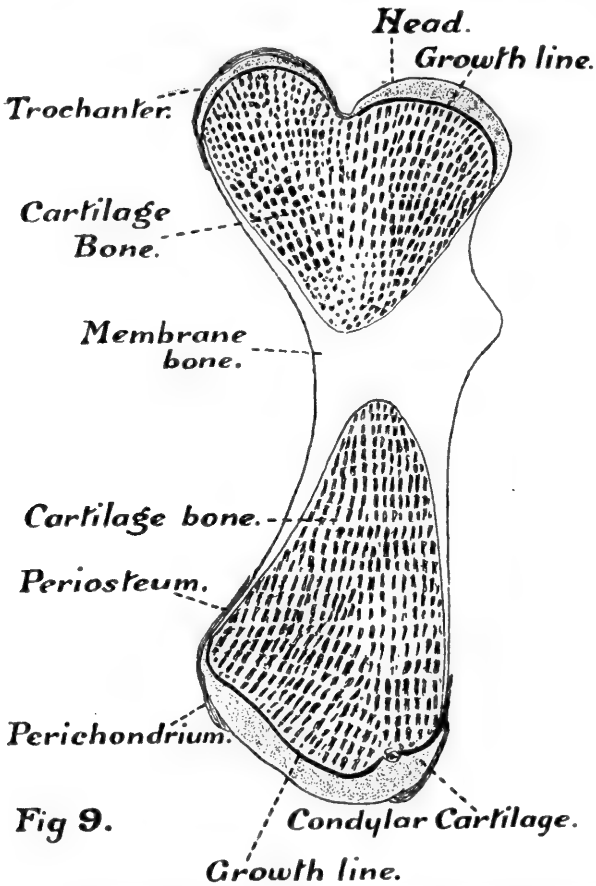


Fig. 9. Vertical section of the femur of a turtle (*Chelone mydas*) showing periosteal or membrane-formed bone encasing the medullary cones of cartilage-formed bone. From a specimen in the R.C.S. Museum.

In Fig. 10 a drawing of the skiagraph of the distal end of the left femur of Dorothy D., aged 16 (Mr Bristow's case), is reproduced. The dense bone of the shaft, representing periosteal deposit, is seen to terminate quite abruptly in an upturned edge. Below the upturned edge is an open cancellous network, which I suppose to be endochondral-formed bone. The drawing represents the condition in December, 1919; in February of that year an identical skiagraph was taken; the diaphysial outline at that date is represented by a stippled line in Fig. 10; it will be seen that new bone has been added not only

in the cartilaginous growth disc of the diaphysis (to a depth of 3·5 mm.) but also along the whole of the medial surface below the upturned edge of the dense periosteal bone. On the lateral surface there has been a certain degree of absorption (see Fig. 10). Apparently the upturned periosteal margin of bone had remained stationary; it had not descended towards the distal end of the shaft during the period under observation. Yet when we compare this skiagraph with those of the older cases shown in Figs. 1, 3, and 4, we must presume that at the end of adolescence the modelling process does proceed and that the exposed cancellous bone becomes irregularly covered by dense bone of periosteal origin. It will be seen that the supposition that there is an arrest of development in the periosteal ring of the diaphysial growth disc explains the appearances presented by the shafts of long bones in Diaphysial

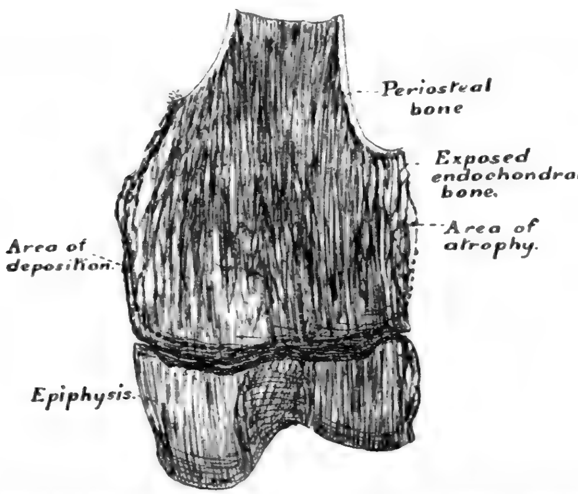


Fig. 10. Distal end of the left femur of Dorothy D., aged 16, a subject of Diaphysial aclasis. The stippled line indicates the outline of the skiagraph of the diaphysis taken ten months previously. The area outside the stippled line represents the growth of the last ten months.

aclasis. The arrest in the extension of the periosteal ring permits the cartilage of the diaphysial disc to become exposed on the surface of the shaft and thus leaves it uncovered and free to give rise to irregular outgrowths or exostoses. A covering of periosteal bone exercises a restraining or a controlling influence on endochondral bone.

Unfortunately I have not had an opportunity of studying the microscopic changes which occur in the diaphysial growth disc of the subjects of this disorder. These discs, as seen in skiagraphs, are more irregular, more dentated than in normal growth; there is a certain resemblance to the changes seen in rickets. It is very possible that besides the arrest of extension of the periosteal sheath, there is also an irregular grouping and division of the cartilage cells. Indeed I am inclined to suspect that the primary disturbance may prove to lie in the growth behaviour of the cartilage cells.

In about one-third of the cases reported—some 300 in number—there is a dislocation of the proximal end of the radius—a result of unequal growth between the bones of the forearm. In such cases, it will be found that the ulna ends above the wrist in a thimble-shaped mass of cancellous bone. In the two cases represented in Fig. 11 all trace of the distal epiphysis of the ulna has gone; in one of Mr Laming Evans' cases, a girl of 17, this epiphysis, although separate and apparent, is clearly being absorbed. The disappearance of the distal epiphysis of the ulna does not account for the arrest of the growth in length of the diaphysis of that bone; it merely shows that there is a profound disturbance of growth at the distal end of the ulna. The radius has a growth disc at each extremity of its shaft. Prof. Digby[1] estimates that 25 per cent.

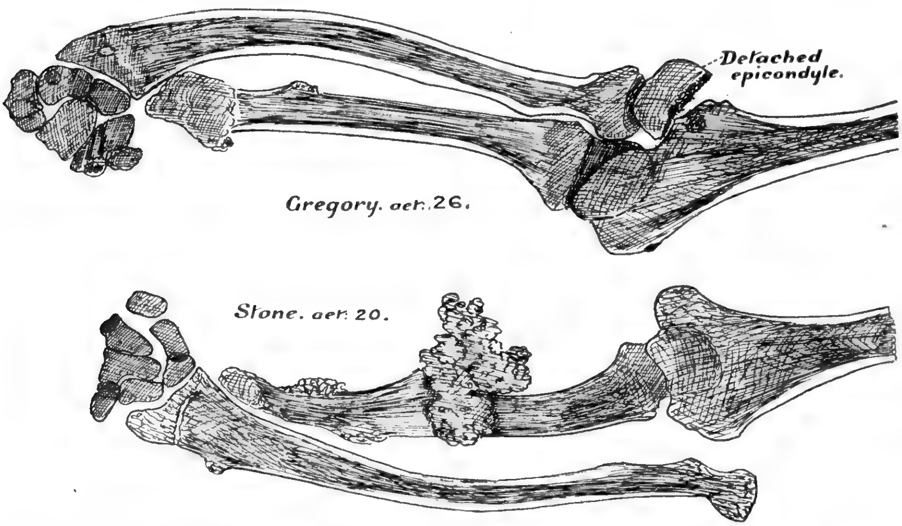


Fig. 11. The upper figure represents a dislocation of the proximal end of the radius with detachment of the lateral epicondyle in the right arm of Capt. West's case, as a result of arrested growth at the distal end of the ulna. The lower figure represents a corresponding dislocation in the left arm of Capt. Annan's case.

of its growth in length takes place at the proximal disc; 75 per cent. at the distal. In the ulna, he estimates that the distal line is responsible for 81 per cent. of the growth. A disturbance of the distal growth disc will therefore affect the extension of the ulna much more than the extension of the radius. In Fig. 12 are represented skiagraphs of the distal ends of the radius and ulna of Dorothy D., aged 16. In her, there has been no dislocation of the proximal end of the radius; the shortening of the ulna is decidedly greater in the right arm than in the left. The stippled areas represent, in Fig. 12, the deposit of bone during the previous ten months. At the distal end of both ulnae the new deposit surrounds the cancellous extremities; it is as great at the sides of the terminal shaft as in the terminal diaphysial line. I infer that the diaphysial

[1] *Journal of Anatomy*, 1916, vol. L. p. 187.

growth, in place of being confined to the diaphysial line, has become spread out over the surface of the cancellous extremity; the cartilaginous disc has been spread out, as it were, over the sides as well as over the terminal surface of the shaft. The cartilaginous growth disc has become diffused. But there is evidently some other circumstance, not yet mentioned, which causes a greater degree of repression of growth in the ulna than in the radius. We know that stresses and strains have an influence on the activity of bone corpuscles and I suspect that as the radius is subjected to these strains and stresses more than is the ulna, that the growth of the latter bone suffers to a greater degree. In Diaphysial aclasis there is a shortening of all the long bones. In the St Thomas's Hospital case the humerus is least affected; its total length is 312 mm. on the right side, 299 mm. on the left. The right radius is 199 mm., the left 191 mm. In proportion to the length of the humerus the length of the radius ought to have been about 230 mm. There has been a loss of about 15 per cent. in its total growth in length. In the ulna there is a deficiency, as regards length, of 26 per cent. But even when we have taken all of these factors into account there is still some factor militating against the growth in length of the ulna in Diaphysial aclasis which remains to be discovered. The fibula also tends to lag behind the tibia, but the union of opposing exostoses and the consequent fusion of the terminal shafts prevent any great discrepancy in their respective growths.

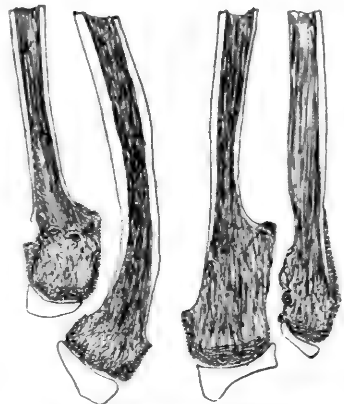


Fig. 12. Tracings of the skiagraphs of the distal ends of the forearm bones of Dorothy D., aged 16 (Mr Bristow's case). The stippled areas represent the bone deposited during the previous ten months.

In the lower drawing of Fig. 11 it will be seen that a large exostosis grows from the shaft of the ulna a short distance below its mid point. The root of this exostosis descends towards the distal extremity of the shaft. It is the presence of the outgrowths from parts of the shaft, very remote from the diaphysial growth discs, that has led clinicians to think that cartilaginous exostoses cannot be a product of the cartilaginous growth discs. The youngest subjects of this condition, so far reported, have been in their second year but when we see how large a number have inherited this disorder of growth and grasp the true nature of the disease we are justified in supposing that in every case the condition, or a tendency to produce it, is already present at birth, although it is not until the eighth or tenth year that it becomes manifest by the painless development of bony outgrowths. In the majority of cases the acute phase of the disease commences with the ripening of the genital glands. Now the point at which an exostosis is situated in Fig. 11 corresponds to the position of the distal extremity of the diaphysis of the ulna in the first or

second year after birth. The largest exostoses are always those which spring from near the middle of the shaft and I regard them as parts or areas of endochondral-formed bone detached from the growth disc while that structure was still replete with the potential growth of infancy. Even the large exostoses usually cease to grow when adult years are reached—when epiphyses become fused with their respective shafts. We have, in the existence of mid-shaft exostoses, evidence of the early onset of the disorder. In Diaphysial aclasis the radius becomes a bent bow; the ulna serves as its taut string. In about one-third of the cases the bow becomes unbent by a spontaneous dislocation of the proximal end of the radius.

In Fig. 13 the distal ends of the left tibia and fibula of Dorothy D., aged 16, are represented. In Fig. 13, A, the condition is shown in February, 1919; in

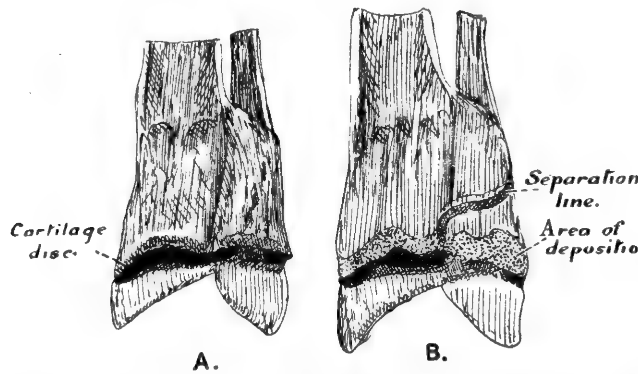


Fig. 13. A. The distal ends of the tibia and fibula of Dorothy D., aged 16 (Mr Bristow's case). The cartilaginous growth discs are indicated by irregular black bands. The terminal diaphysis of the tibia has expanded laterally and apparently fused with the terminal expansion of the fibula.

B. A drawing of the same parts ten months later. A line of separation now marks off the lateral expansion of the tibia. The stippled area indicates the deposit of the previous ten months.

Fig. 13, B, the condition in December of the same year is represented. The stippled area represents the new bone added in that interval; it lies entirely within the diaphysial line. In the earlier skiagraph the lateral expansion of the terminal shaft of the tibia has apparently fused with the bone of the fibula, but in the later skiagram a sharp separation has occurred between them. The fibula has apparently undergone a slight dislocation laterally for the total breadth, from the medial border of the tibia to the lateral border of the fibula, has increased about 4 mm. In Capt. West's case, a man aged 26, there is a medial outgrowth from the fibula which has pressed against the expanded end of the tibia and caused a wide area of superficial absorption, the cup-shaped area thus excavated being lined with a layer of indurated bone.

Each bone reacts in the subjects of Diaphysial aclasis in a characteristic manner. The distal end of the humerus rarely shows more than a slight dis-

turbance of growth while its proximal end is almost the first site to give an outward manifestation of the presence of the disorder. Prof. Digby estimates that 81 per cent. of the length of the shaft of the humerus is added at the proximal diaphysial line and we may therefore expect a much greater degree of disturbance at this extremity. In Fig. 14 I give drawings from the skiagraphs of the shoulder region of Dorothy D., aged 16. The terminal unmodelled part of the shaft of the left humerus measures 64 mm. in length by 35 mm. in width (as measured in the skiagraphs). The sleeve of dense periosteal bone ends quite abruptly where the cancellous cylinder begins. The deposit of new bone,

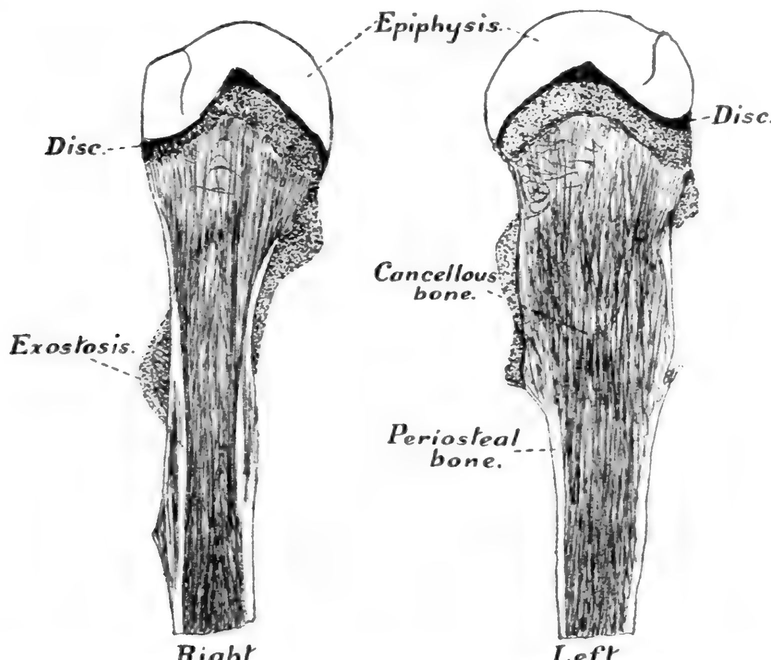


Fig. 14. The proximal ends of the right and left humeri of Dorothy D., aged 16 (Mr Bristow's case). The stippled areas represent the bone deposited during a period of ten months. The diaphysial growth discs are represented by thick black lines.

represented by the stippled areas, has been almost entirely laid down in the terminal diaphysial line (forming a stratum 6 mm. in depth) but certain deposits have also been added to the lateral and medial surfaces of the terminal shaft. In the right humerus (Fig. 14) the modelling process, although interrupted, has proceeded almost to the diaphysial line. Yet in spite of the greater intensity of the modelling process in the right bone there has been a heavy deposit of bone outside the terminal surface of the shaft. The recent deposit on the lateral aspect is plainly an exostosis growing from the pectoral ridge. It is also likely that the deposit on the medial surface is not laid down over the dense casing of periosteal bone—as it appears to be in the skiagraph—

but is really of the nature of an exostosis or deposit growing on the extensor aspect of the shaft. There can be no doubt as to the irregularity of the process of growth which is taking place at the proximal ends of the humeri nor of the partial arrest of the modelling process.

The figures used to illustrate this paper represent the typical growth lesions of the long bones. The clavicles, ribs, scapula and os innominatum show corresponding defects and excesses of growth. Further observation will probably reveal lesions in the base of the skull.

There is one other growth lesion which is very closely related to the disorder named here Diaphysial aclasis. If the law which I have laid down that in this disease every bone in the body which is made up by the union of endochondral and periosteal elements exhibits aclasis and overgrowth be true, then we should find the shafts of the metacarpal and metatarsal bones and of the phalanges of the fingers and toes also showing similar disturbances. The metatarsal and metacarpal bones do occasionally show a slight degree of the disorder—particularly those of the fourth and fifth digits—but both metacarpals and metatarsals and their phalanges are usually quite normal in their growth. In those cases however where the derangement is apparent before the sixth year the long bones of the hand and foot are affected. On the other hand these elements of the hand and foot are subject to another disorder, also hereditary in nature and occurring in infancy and youth, namely multiple enchondromata. These localised cartilaginous tumours arise within the shafts of phalanges and metacarpal and metatarsal bones—particularly those of the 2nd and 3rd digits. All of these bones are peculiar in their order of ossification; the periosteal sheath of bone is laid down almost before the cartilage core has commenced to ossify. I expect that a re-investigation of the developmental processes attending the ossification of these long bones of the hand and foot will throw light upon this bizarre anomaly of growth.

The conception of multiple exostoses as a disorder of growth is not new. John Hunter recognised that it was "constitutionally interwoven with the formation of bones in some people" (Palmer's Edition, vol. I. p. 533). Sir James Paget expressed a somewhat similar opinion when he wrote of multiple exostoses: "Indeed at this point the pathology of tumours concurs with congenital excesses of development and growth" (*Lectures on Surgical Pathology*, 3rd edit., 1870). Bessel-Hagen and Nasse (see references in footnote, p. 106), who have written the best monographs on this disorder, are also inclined to regard it as a growth disturbance. Ollier (*Revue de Chirurgie*, 1900, vol. XXI. p. 39) has described under the name of Dyschondroplasia a condition which is probably only an extreme condition of the disorder named here Diaphysial aclasis.

When we seek to probe beneath the surface and search for the immediate cause of this peculiar disturbance of growth we find no sure foothold on fact. The condition of the various glands of internal secretion in those who are the subjects of the disease has not been studied. Nor when observations are

made do I expect that any gross lesion will be found. Even in Achondroplasia no anatomical change in the structure of the thyroid has been noted and yet from the similarity of the growth lesions in Achondroplasia to those seen in cretinism there is a fairly certain basis for suspecting that a functional defect of the thyroid is the immediate cause of the growth defects seen in Achondroplasia. In certain respects Diaphysial aclasis is contrasted to Achondroplasia and yet it seems to fall into the group of thyroid disorders, for we find that while one defect of the pituitary gland may lead to dwarfism another produces giantism. There can be no doubt that in Diaphysial aclasis we have one of the most remarkable of all known disturbances of growth.

Summary. The disease known to clinicians as Multiple exostoses is a definite disorder of growth and should be named Diaphysial aclasis to indicate the nature of the growth disturbance. It is congenital in point of origin and affects only those parts of the skeleton which are developed from both cartilage and membrane. It is related to Achondroplasia and there is reason for suspecting that it may be due to a disturbance in the function of the glands of internal secretion—the thyroid gland being the one which is most likely to be at fault. The study of this disorder helps us to analyse the normal machinery of bone-growth.

FUNCTIONS OF THE LIVER IN THE EMBRYO

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A strange statement was made by Harvey in the sixteenth chapter of his immortal *Exercitatio Anatomica de Motu Cordis.* He says here: "Hinc in Embryone pene nullus usus jecoris, unde...etiam in prima foetus conformatione jecur posterius fieri contingit, et nos etiam in foetu humano observavimus perfecte delineata omnia membra, imo genitalia distincta, nondum tamen jecoris posita pene rudimenta...."

One cannot help wondering whether the meaning which appears here on the surface really expresses Harvey's intention, and that he meant to convey the impression that the organ is a small thing and of no account in the earlier months of development; for it does not seem possible that so acute an observer would have been ignorant of the great relative size of the liver in these months. No doubt, from the view-point which he occupied at the time, there seemed to be no necessity for a large organ, which would account for the first sentence quoted above; but, with a man of this calibre, it could not explain the second, and one seems almost driven to assume that he was deceived by the condition of his specimens and the friability of the liver—a very unsatisfactory explanation.

The undeniable fact that the liver is of such great relative size in embryonic life suggests that it performs some function then which is associated with its size. The Galenical concept of the liver as the fount and origin of the blood was seemingly laid to rest by Harvey, but, in a sense, it has stirred again, in the qualitative, if not quantitative, blood-forming activities now known to be at work in the organ. But this function does not account for the size of the early liver. It goes on after the liver has altered its rate of growth, and flourishes even after birth. Also the biliary functions of the gland are not established before the relative maximum size is passed, and it is hard to see any connection between them and the great embryonic growth. There seems, in fact, to be only one thing in the life history of the embryo which is directly associated with the greatest size of the liver, and which is coexistent and coterminous with it: I refer, of course, to the extra-abdominal position of the gut, terminating by its passage into the abdomen and its subsequent growth there. This connection has often been recognised, and the liver has been credited with the pushing of the intestine out of the abdomen at one time, and, on the other hand, has been said to be the main power at work in pulling it back again later on, but there has not been, so far as I am aware,

anything more than general suggestions that these things may be so, nor any coherent effort to show by what means they could be so. When working with Dr Robbins on the rotation of the gut, I found myself adopting more defined and, I think, reasonable views about the part played by the liver in the matter. In the paper published at the time in this *Journal* I mentioned these views shortly, in so far as was necessary for the purpose in hand: in this communication I propose to give a fuller account of what, in my opinion, this part may be considered to be.

For convenience, the subject may be considered under several different headings.

1. *The state of the embryonic liver*

As is apparent at once on examining sections, the liver of the embryo is a loosely built organ, very vascular. It consists of solid material and a considerable amount of fluid. The solid portion, leaving out of account blood cells which vary directly with the amount of blood, is a fixed quantity. The fluid constituent of the liver can be divided into that within the vessels and that outside them. The former, the blood, can by its escape into its natural extra-hepatic and extra-abdominal channels, lead to a rapid and sensible diminution in the total bulk of the organ, the unchanged quantity of solid constituent remaining. The liver grows by increase of its solid columns and of the vascular spaces between them. It grows in correspondence with the growth of the abdominal cavity, and fills up every available corner of that cavity, lying beside the median mesenteric septum and the bursa omentalis. But there does not seem to be any reason to suppose that in its growth it exercises any pressure whatever on neighbouring structures: on the other hand, reasons for thinking that it does not do so may be seen in the state of the bursa omentalis, the bold transverse curve of the duodenum, the processes of the Wolffian bodies, the thin-walled veins in the organ and outside it, etc. I am not aware of any evidence of pressure being exerted by the growing liver, and, during the examination of all stages, the impression has formed itself in my mind that the organ in its growth might almost be likened to a very viscid fluid slowly running, without pressure, and flowing into interstices and filling up spaces: of course it is not a simple viscid fluid, but such an idea will illustrate fairly well, in some ways, the conception I have formed of its mode of growth and the way it acquires its form. It is instructive to examine places where (as may be seen for instance here and there beside a well-developed Wolffian body) a process of the liver has passed in through some narrow chink or fissure, into a wider space, so that a small enlargement is torn off at its narrow neck when the organ retracts on dehydration: in these cases there has plainly been extension of the liver without any flattening of the structures bounding the chink, as if the liver had "flowed" into the recess rather than pushed its way into it.

The conception of a liver growing in this way, composed of solid columns with intervening spaces filled with fluid which is able to vary in amount,

entails certain corollaries. The growth goes on *pari passû* with the growth of the belly cavity: but if the solid parts grow faster than the cavity, it follows that the fluid parts must become relatively less, and *vice versâ.* So, if we accept the general truth of Jackson's statements about the falling rate of growth of the liver after the first part of the third month, it means that the venous spaces in the organ at this time are comparatively large, and getting relatively larger as the rate falls.

2. *The mechanical bearing of this state*

I have, so far, seen no reason to believe that the liver is in any way responsible, through its increase in size, for the presence of the gut in the umbilical sac. I have not been able to satisfy myself about the matter, principally because my earlier specimens (under 5 mm.) are not sufficiently well preserved to provide reliable data, but I have a decided impression that the extra-abdominal position of the gut has more to do with the slow growth of the belly-wall than with any intra-abdominal condition: that there is no room in the abdomen at first for anything but the Wolffian bodies and the umbilical veins: that this is due to the small size of the cavity from the small extent of the walls: that consequently the lengthening intestinal bend is effective only in the direction of the vitello-intestinal duct: and that the formation of the dorsal mesentery, when its explanation is given, may possibly throw more light on the umbilical position of the gut than will any researches on the liver. Or, from a point of view a little different, it might be said that the abdominal wall closes in behind the umbilical gut, and thus this part of the bowel is not extruded from the belly, but lies outside it *ab initio.* Whether these views turn out to be true or not, there is little doubt that the gut is already outside the belly wall by the time the liver begins its most effective growth, and, to my mind, this growth is called forth by, and is an expression of the necessity for filling the space caused by, the increasing area of wall—increasing too late to enclose the bowel within it. In other words, the liver growth would be more rightly looked on as an indirect consequence of the external position of the gut, than as the cause of the gut assuming this position.

But, though it may not cause the extrusion of the bowel, it would seem that the presence of the growing liver leads to the continued extra-abdominal existence of the viscus. The organ grows *pari passû* with the cavity, which it fills, so that the walls are supported by it against the external amniotic pressure. This equalisation of pressure permits the other viscera, whether inside or outside the belly, to live in "a state of rest" in their respective situations.

There can only be inverse variations between the two constituents of the liver mass, if this is to keep pace with the growth of the cavity: such variations will naturally only be possible within limits. So long as the limits are not exceeded, or perhaps too closely approached, the condition of equilibrium

between the internal and external viscera will remain: if one could imagine such a thing as the liver failing altogether to develop, while the abdominal walls grew at their usual rate, it would not seem possible that the formation of the intestinal coils could go on outside the cavity; for the cavity must be filled, and, if the liver fails to perform this function, it can only be carried out by the intestine. Looking at it conversely, the development of the coils outside the belly is an indication that the liver growth fulfils efficiently the task of occupying the available cavity and equalising the intra-abdominal and extra-abdominal pressures.

3. *The mechanical state towards the end of the first stage*

Towards the end of the first stage, when the umbilical gut is nearly ready to enter the abdomen, the rate of growth of the liver, i.e. of course, of its solid parts, begins to fall behind that of the cavity. This was pointed out by Jackson some years ago (*Anat. Record*, 1909) and there can be little doubt, I think, that his general conclusions are correct, although, as we shall see later, there may be reason for modifying the details of his figures. As the rate of solid growth falls, and as the mass must still fill the cavity, it follows that the relative amount of blood in the organ must be increased: it is evident that, the decreasing rate of solid growth persisting, there will be both actual and relative increase in the amount of blood, and distension of its vessels. One can imagine that at first this change in the relations between solids and fluids would not make itself felt away from the liver, and that then any indications of difficulty in keeping pace with the growth of the cavity might be met by falling in of the walls to some little extent, but, if the process continues, there must come a time when the vessels and the solid columns between them are stretched to their utmost extent, and any further reply to the demands of the growing cavity becomes impossible. Whether the process ever does proceed so far as this or not, I have no means of deciding, nor does it really much matter from our present point of view; it is sufficient to understand that the liver now contains a large and unusual amount of fluid, and may be considered to be "stretched" to a considerable extent, a condition necessarily associated with lessening of the tension inside the abdomen, compared with that outside it and away from liver influence.

4. *The necessary conditions associated with the entrance of the gut into the abdomen*

This movement of the intestine is rapid. As I conceive it, it is probably only a matter of minutes. It is brought about by a *relative* rise in extra-abdominal pressure, due to some fall in intra-abdominal tension. The mass of gut and mesentery in the sac may perhaps offer at first some resistance to the movement, aided by the small size of the aperture through which they must pass, but when once the movement starts there is no reason why it should not continue. The nature of the movement and its order have been already dealt with in the previous paper, and need not detain us now.

It is evident that the introduction into the abdomen of such a comparatively large mass as that which occupies the umbilical sac calls for provision of space for special accommodation. This space must be provided as it is required: it cannot exist as an unoccupied part of the cavity before the entry of the intestines, for this would mean either a vacuum or a collection of fluid which would change places, so to speak, with the gut, a supposition at variance with the mechanical causes of the entry on the one hand, and, on the other, with the conditions of both umbilical and abdominal regions as found in the embryo. Moreover, it seems necessary to suppose that the provision of the space must take place without the exercise of any force on the part of the intestine: the gut cannot be thought to compress any organ or organs which it finds in the abdomen, for this would mean that it makes its way against resistance, a thing hardly conceivable.

I suppose that a common idea of what takes place might be expressed by saying that the lessened growth of the liver and Wolffian bodies leads to a fall in "intra-abdominal tension" which is met by the walls falling in below the liver; then, when the gut comes in, space is provided by the bulging of the slack of the walls. To my mind this conception is open, without considering other points, to the fatal objection that it does not allow for the play to their end of the factors causing the movement. Even if one were to admit—which I would hesitate to do—that such elastic recoil were possible in these walls, a little reflection will show that the exercise of this quality by the walls is not compatible with a complete return of the intestine: the force supposed to be leading to the return would decrease rapidly as the walls were relieved of their inverted strain by the incoming bowel, a state of quiescence ought to occur very soon, and it is impossible to conceive the movement going on to a bulging of the walls, unless we postulate an insistence (on the part of the bowel) on finishing the job when it has once started to enter the belly—a form of vital activity hitherto unsuspected. For my part, I cannot help feeling that the walls are incapable of playing any but a subsidiary part in the movement, and that they are mainly passive so far as it is concerned, perhaps indirectly aiding (as will be mentioned later) in the beginning of the movement, but exercising no influence on its continuation or completion.

We might say, then, that the explanation of the conditions immediately preceding, accompanying, and following the ventralisation of the bowel must take account of the necessity for providing potential accommodation, for converting this into actual accommodation as and when it is required, for allowing this to take place without calling for any pressure from the bowel, and for connecting all this with the mechanism which leads to the intra-abdominal movement of the gut. In addition, the factors causing the change of location must be capable of continuous action till the movement is completed.

5. *The rôle of the liver in meeting these necessities*

It has been pointed out above that the liver, if its rate of growth falls and it yet fills the cavity, must be in what can be conveniently termed a "stretched" state as the end of the first stage approaches. With certain and evident reservations, it may now be likened to the lung in the adult thorax, a viscus also in a "stretched" condition. The lung exercises a pull on the thoracic wall which is increased as the thorax is enlarged: this is the same as saying that the intrapleural pressure is further lowered. So long as the liver grows *pari passû* with the belly its conditions differ from those of the lung, but when it becomes "stretched," it is comparable with that organ: it begins to exercise a pull on the abdominal walls, and, as these enlarge, the intra-abdominal pressure is lowered. If a tube were inserted into the pleura, water or air would be drawn into that cavity through it when the thorax enlarges: in the case of the abdomen there is already an umbilical tube connected with its cavity, and its contents similarly tend to be drawn into the abdomen as the intra-abdominal pressure falls: these contents are coils of gut and mesentery. The immediate cause, then, of the ventralisation of the intestine is the relative increase in external pressure arising as the result of lowered internal pressure, due to the "stretched" state of the liver as the walls grow.

Also, as the pull of the lung would not be satisfied by the passage through the tube of a few drops of water, but would lead to the taking in of a quantity sufficient (if obtainable) to allow its collapse, so the retraction of the "stretched" liver would continue in front of the entering intestines, without pressure from them and merely in virtue of its own power of recovery of its natural "unstretched" condition. This, it is hardly necessary to point out, implies that the excessive blood occupying the dilated spaces is expelled from the liver into the vena cava, so that the organ is reduced in size and the original relation between solids and fluids restored. Thus it may be said that the intestinal presence enables the liver to retract, and it is the tendency to retraction, essentially inherent in its distended and "stretched" condition, which initiates and carries on the movement of the bowel. Hence the liver might be described as retreating before the intestine, without pressure, as a lung retreats when some foreign substance begins to occupy the pleural sac.

Whether the tendency to retraction is wholly satisfied or not by the presence of the gut is, of course, a matter at present impossible to decide. The rapid growth of the bowel after the event seems to point to an answer in the negative, and it is conceivable that the dorsal shifting of the originally umbilical colon may indicate the same. The apparent rapidity of the movement and its complete nature, with the great rarity of partial failure, also point in the same direction, unless we are willing to admit a most accurate and delicate adjustment between the retractile potentiality and the intestinal mass.

Unfortunately, and in the nature of things, it is only possible to bring

forward as assumptions the functions which are claimed here for the liver. Experimental proof of the assumptions is, of present necessity, lacking. I hope that it may be possible to carry out some experimental observations on other embryos when the opportunity serves, but, as nearly all my human material reaches me in formalin or alcohol, it has not been possible to use it in this way. But the examination of ordinary prepared specimens yields certain results which are of importance in this connection.

In the first place, there can be no doubt that the liver occupies all available space in the abdomen of the living or recent embryo. Reconstruction models show this clearly: for example, the model of the liver of a 28 mm. specimen, made for the original work, demonstrates by its markings all the organs with which it was in contact before dehydration. In this way it can be shown indubitably that, as in all other specimens after the youngest, it reached to the extreme caudal limit of the abdominal cavity: yet the sections exhibit the lower portion of the cavity as quite free from any trace of liver structure. This is the usual and necessary concomitant of preparation. Dehydration of the liver implies its contraction through the removal of fluid, and, as its attachment is above, its retraction must show its effect mainly below. It follows from this that, though the shape and relational markings are fixed and preserved with a general fidelity, the bulk of the reconstructed organ is less than it should be if it is to be taken as an absolute proportionate enlargement of the actual liver, and the ratio of its mass to the abdominal cubic content is false without considerable correction. It was from this standpoint that I took exception, earlier in this paper, to the acceptance of Jackson's measurements and ratios as calculations accurate in detail. My objection is, of course, only to their acceptance without due correction for the effects of dehydration, and does not apply to his general conclusions. I have tried to avoid dehydration by making use of Salkind's "lead gum" method, but this was not successful in my hands and was abandoned owing to wastage of valuable material: in other hands it might succeed and yield good results.

The shrinkage of the liver resulting from dehydration is very suggestive, in that it shows how space can be provided in the abdomen by loss of fluid from this organ. But the conditions under which fluid is removed in this case differ widely from those that would be present if fluid were taken out as blood, through the vessels. In the first case the alcohol replaces the water in the vascular spaces, so that no collapse of these spaces takes place, while its action on the solid columns is further modified by their previous fixation: in the second case there is nothing to replace blood withdrawn, so that, if it is withdrawn, the solid material round the spaces must fall in, and the total bulk of the liver must be decreased by so much. It would seem, then, that the contraction due to dehydration would not be so marked as that brought about by the withdrawal of a relatively small quantity of intravascular blood, and the possibilities of this last method are, of course, much greater; indeed, the maximum effect would be produced by complete

exsanguinification of the organ, a process which never occurs but which, if it did occur, would probably lead to reduction to about half the original bulk.

The following observation is of interest in connection with this aspect of the condition. Two models were made from an embryo of a stage just preceding that in which ventralisation of the bowel might be expected to occur. One was a "cast" of the abdominal space from which the liver had retracted, care being taken to cut wide of the various structures there and not to include any part of the space which seemed in any way to have come into being as between two organs originally in contact, so that as far as possible only the effect of liver contraction might be gauged: if any doubt arose, it was always decided against the inclusion in the model of that part of the cavity concerned, and in this way a cast was obtained which was not, I think, larger than the liver space required, but was in all probability considerably smaller. The second model represented the umbilical mass of gut and mesentery: to obviate the shrinkage of these, the outline of the containing sac was taken in place of its contents, as these had during life filled the sac, and in this way a mass model was obtained which might with great fairness be said to be approximately equal to—if not larger than—the bulk of the contents of the sac during life. The bulk of each model was then found by displacement. The result gave the ratio between the cavity and the umbilical mass as 28: 31. As already stated, the first measurement is probably too small, and the figures, I think, would more truly be expressed as about of the same value, but the interest of the observation really lies in the indication afforded by it of the amount of contraction which occurs in the liver as the result of extraction of fluid. It is evident that the necessary accommodation for the incoming intestine could be provided, probably altogether, by shrinkage as the result of removal of fluid from the solid columns, and hence it would seem that it could be obtained easily by the more definite and complete retraction got by withdrawal of blood from the liver vessels, if this withdrawal takes place: if the withdrawal does not take place, there does not seem to be any mechanism through which the liver can lessen its bulk, and lessening of its bulk is absolutely necessary if the intestines are to find place in the abdomen.

These points just mentioned are important ones, as they bring forward the fundamental facts on which comprehension of the mechanical conditions depends: the abdominal cavity is fully "occupied" up to the entry of the gut, it must be occupied during the passage, and yet accommodation must be provided—and of all the structures which affect the cavity the liver is *the only one* even remotely capable of fulfilling these functions.

If the views advanced in this paper are confirmed by further experience and prove to be substantially correct, we have in them some explanation or reason for the rapid rate of growth and size of the liver in the embryonic period: it allows the abdomen to grow while the intestine develops outside it, it supplies the means by which the intestines are brought into the belly,

and it provides the accommodation for them therein, as and when it is wanted. No suggestion is offered concerning the apparent necessity for the extra-abdominal development of the gut; it is even conceivable that this position of the bowel is required, for some deeper reason, to allow the liver to develop. But, however this may be, there is in my mind no doubt about the mechanical relationship between the two conditions, as set forth above. This way of looking at the questions seems to me to offer the only completely satisfactory solution of their problems, congruous with all the conditions present.

We might therefore divide the intra-uterine life of the liver into two main stages: the *embryonic*, in which its functions, other than growth, might be termed mechanical, and the *foetal*, after the ventralisation of the bowel, when the processes of bile-formation and of other bio-chemical activities are initiated.

The excessive development of the liver in its early stages has now some sort of *raison d'être*; it is otherwise apparently meaningless, for we see even atrophy and degeneration of some parts at later stages. Moreover, not only is the accuracy of the general statement quoted from the *Exercitatio* upset by the fact that the liver reaches a great size in the early stages, but the reasons advanced for this great size, if they are accepted, dispose of the particular assertion contained in the first sentence of the quotation. There can be no question about the truth of the statement that the gut is extra-abdominal and becomes intra-abdominal, nor that the mechanical conditions underlying and allowing these states and changes call for explanation, and, as already stated, the only completely satisfactory and satisfying explanation would seem to be that which brings in the liver in the ways advocated in this paper.

ON THE DEVELOPMENT OF THE HYPOBRANCHIAL AND LARYNGEAL MUSCLES IN AMPHIBIA

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The adult anatomy of the laryngeal muscles, nerves, and cartilages, in Amphibia is now well-established, and especially by the work of Henle, Fischer, Wilder, Gegenbaur, Göppert, and Drüner. An explanation of the facts observed was sought for, and in 1892 the theory was put forward that the laryngeal muscles are branchial in origin, their nerves branchial nerves, and their cartilages modified branchial bars. A short history of the rise of this theory and of its modifications forms a preface to this paper.

In papers published in 1916 and 1919 I showed that in Mammalia and Sauropsida the laryngeal muscles, other than the Crico-thyroid of Mammalia, are developed from the Constrictor oesophagi. In this paper evidence is adduced that in Amphibia, similarly, the laryngeal muscles are developed from the Constrictor oesophagi and are not derivatives of any branchial-arch musculature.

The larynx in Amphibia comes into relation with certain hypobranchial muscles, and a description of their development and morphology precedes that of the laryngeal structures.

Many names have been employed by writers. A uniform nomenclature has been used in the following paper, both in the historical account and in the record of observations; and the following tabular statement shows its relation to the names employed by previous writers.

Ventral muscles of the branchial arches.

In this paper:		
Transversi ventrales:		
Urodela:		
Transversus ventralis iii of Necturus and Proteus	Fischer	Hyo-trachealis
Transversus ventralis iv of other Urodela	Wilder	Hyo-laryngeus and Hyo-trachealis s. Pharyngo-branchialis iii or iv
	Gegenbaur	Hyo-trachealis
	Göppert	Hyo-pharyngeus s. Hyo-trachealis
	Drüner	Interbranchialis iii or iv
Anura: larva		
Transversus ventralis iv	Göppert	Hyo-pharyngeus
Gymnophiona:		
Transversus ventralis iv	Göppert	Hyo-pharyngeus.

Subarcuales recti and obliqui:		
Urodela:		
Subarcualis rectus i	Fischer, Mivart Miss Platt, Drüner	Ceratohyoideus internus
Subarcualis obliquus ii of Necturus and Proteus	Fischer	Adductores arcuum
	Miss Platt	Constrictor arcuum
Subarcuales obliqui ii and iii of other Urodela	Drüner	Adductores branchialium
		Subarcuales obliqui
		Ceratohypobranchialis (in Necturus and Proteus)
		Constrictor arcuum branchiarum
Subarcualis rectus iii of Necturus and Proteus	Fischer, Gegenbaur, Mivart, Miss Platt	Constrictores arcuum
	Drüner	Subcerato-branchiales
Subarcualis rectus iv of other Urodela	Göppert	Constrictores arcuum branchialium
	Drüner	Subarcuales recti
		Constrictores arcuum branchialium
Anura: larva		
Subarcuales recti i and ii	Dugès	Ceratobranchial
	Schultze	Ceratohyobranchialis
Subarcuales recti iii and iv	Schultze	Interbranchialis
Gymnophiona:		
Subarcualis rectus i	Fischer	Ceratohyoideus externus
	Fürbringer	Ceratohyoideus
	Norris and Hughes	Ceratohyoideus internus
Subarcuales recti ii, iii and iv	Fischer and Göppert	Constrictor arcuum branchialium

Laryngo-tracheal skeleton

	Whole cartilage	*Anterior part*	*Posterior part*
In this paper	Cartilago lateralis	Pars laryngea s. arytenoid	Pars trachealis
Urodela:			
Henle (1839)	—	Cartilago s. Pars arytaenoidea	Cartilago s. Pars laryngo - trachealis s. Cartilago lateralis
Fischer (1864)	—	Seitenknorpel	—
Wilder (1892 and 1896)	—	Arytenoidea s. C. lateralis	Tracheal elements
Gegenbaur (1892)	Cartilago lateralis	Arytenoidea s. Stellknorpel	—
Göppert (1894 and 1898)	Cartilago lateralis	Pars arytenoidea	Pars cricotrachealis
Drüner (1901 and 1904)	—	Cartilago lateralis s. Pro arytenoidea	Proc. trachealis
Gymnophiona:			
Henle	—	Cartilago arytenoidea	Cartilago lateralis
Göppert	—	Pars arytenoidea	—
Anura: larva			
Wilder	—	Arytenoidea	—
Göppert	—	Arytenoidea	—
Anura: adult			
Wilder	—	Arytenoid and apical cartilage	{ Annulus Processus bronchiales
Henle	—	C. arytenoidea and C. Santoriniana	C. laryngo-trachealis
Göppert	—	C. arytenoidea and C. Santoriniana	Pars crico-trachealis of { Pars cricoidea Partes tracheales

Laryngeal muscles

	Dorsal laryngeal muscle	*Laryngei*	*Constrictor muscle*
In this paper	Dilatator laryngis	Laryngeus dorsalis Laryngeus ventralis	Constrictor laryngis
Urodela:			
Henle	Dilatator aditus laryngis	—	Constrictor aditus laryngis
Fischer	Dorso-laryngeus and Dorso-trachealis	—	Constrictor aditus laryngis
Wilder	Dorso-laryngeus and Dorso-trachealis s. Dorso-branchialis v.	Laryngei	Ring of Periarytenoideus dorsalis and ventralis
Gegenbaur	Dilatator aditus laryngis	—	—
Göppert	Dorso-pharyngeus of Dorso-laryngeus and Dorso-trachealis	Laryngei	Sphincter laryngis
Drüner	Dorso-laryngeus	Laryngei	Constrictor aditus laryngis
Gymnophiona:			
Henle	Dilatator aditus laryngis	M. interlateralis	Constrictor aditus laryngis
Göppert	Dilatator laryngis	Laryngeus ventralis Laryngeus dorsalis (?)	Sphincter laryngis
Anura: larva			
Wilder	Dorso-laryngeus s. Dorso-branchialis v.	—	Sphincter laryngis
Göppert	Dilatator laryngis	—	Sphincter laryngis
Anura: adult			
Henle	Oeffner des Stimmladeneingangs	Verengerer des Stimmladeneingangs	Compressor der Stimmlade
Wilder	Dilatator aditus laryngis s. Dorso-branchialis v. s. Periarytenoideus dorsalis	Constrictor aditus laryngis s. Periarytenoideus ventralis	Compressor aditus laryngis Sphincter dorsalis
Göppert	Dilatator laryngis	Hyo-laryngeus	Sphincter anterior Sphincter posterior
In this paper		Constrictor laryngis posterior	

HISTORICAL ACCOUNT

Ventral muscles of the branchial arches

Anura. The Subarcuales recti of the larva were described by Dugès and by Schultze.

Another muscle was described by Göppert (1894) in a 11 mm. larva of Rana, arising from connective tissue surrounding the post-branchial body and passing inwards towards the middle line. In older larvae the median ends of the two muscles meet. He homologised this muscle with Transversus ventralis iv of Urodela and, further, stated that it becomes the Constrictor laryngis posterior of the adult—a muscle which arises from the processus postero-medialis and passes inwards and forwards to meet its fellow in a median raphé just in front of the Cartilagines laryngis.

Wilder, on the other hand, stated (1896) that the Constrictor laryngis posterior develops at a late larval stage (one with rudimentary hind limbs)

as a derivative of the ventral half of the Constrictor laryngis and is not identical with the larval muscle described by Göppert, which probably atrophies. Göppert in 1898 adhered to his previous statement. Neither investigator gave any figures in support of his opinion.

Differences of opinion between Göppert and Wilder in regard to Levator arcus branchialis iv are mentioned later.

Gymnophiona. The Subarcuales recti and the Transversus ventralis iv were described by Fischer and Göppert (*vide infra*).

Urodela. The larynx, owing to certain developmental changes, which will be described later, comes into relation with the Transversus ventralis (iii in Necturus and Proteus, iv in Urodela with four branchial bars). The linea alba, connecting the two halves of this muscle, underlies the pharynx and anterior part of the larynx in Siredon, Salamandra, Triton, Necturus, and Proteus; it underlies the larynx in Ellipsoglossa, and underlies the trachea in Menopoma, Megalobatrachus max. and Amphiuma. Various opinions have been expressed as to the morphology of this Transversus ventralis. Fischer (1864) considered that it was part of a single muscle system—that of a Constrictor pharyngis. Wilder (1892) described the Dilatator laryngis and Transversus ventralis as "extrinsic" laryngeal muscles. He homologised the former with the dorsal segment of the fifth branchial arch of Selachians, but could not determine whether the latter was homologous with the ventral segment of the same arch or not. Gegenbaur (1892) homologised the Transversus ventralis with the Constrictores arcuum of the branchial skeleton (called in this paper Subarcuales recti and obliqui). Göppert (1894), accepting Gegenbaur's opinion, stated that the Transversus ventralis was the hindmost member of a longitudinal series binding together the hyoid and the branchial bars, though differing from the other members in that it has generally given up its ventral attachment to skeletal parts. In Necturus and Proteus, where no fourth branchial bar is present, the hinder part of the Transversus ventralis and the Levator iii pass to an inscriptio tendinea separating them, whilst the chief part of the former muscles passes over to Ceratobranchiale iii. In Megalobatrachus max., where the third and fourth bars are absent, the Transversus ventralis and Levator iii meet in an inscriptio tendinea which forms an anterior continuation of that in the territory of Levator iv. In land-living forms such as Salamandra and Triton, no forward migration of the muscle takes place, and, on atrophy of the rudimentary fourth bar, the Transversus ventralis and Levator iv form a Cephalo-dorso-pharyngeus—a muscle-band with an inscriptio tendinea. Wilder (1896) advanced the theory that, primitively, there was a series of ventral transverse muscles attached to the visceral bars—in the mandibular segment represented by the Intermandibularis anterior, in the hyoid segment by the Intermandibularis posterior, and in the branchial region by a series of Transversi ventrales. In Necturus and Proteus the Transversus ventralis consists of Transversi ventrales iii and iv; in other Urodela only iv is present. Embryology would show whether Transversi ven-

trales i and ii are represented ontogenetically. Wilder made no reference to Vertebrates other than Amphibia. Göppert (1898) accepted Wilder's opinion that the Transversus ventralis of Urodela other than Proteus and Necturus represents a Transversus ventralis iv, but, against Wilder's opinion concerning Proteus and Necturus, stated that the muscle in those animals is an altogether simple one in which no division is possible even in the embryo. Further, no proof had been given that a Transversus ventralis iii as well as a Transversus ventralis iv existed in Urodela with a fully developed branchial skeleton.

Drüner's theory (1901 and 1904) of the segmental origin of the Transversus ventralis of Urodela was different from that of Wilder and Göppert. He found that the muscle is innervated by the N. recurrens intestinalis x, and not by branchial arch nerves. He inferred from this that the muscle had migrated forwards from more posterior segments which once existed and was not native to the segment in which it lay. His terms Transversus ventralis iii or iv are thus purely descriptive and denote merely the bar of attachment. (It may be added that this theory was adopted in all cases of the hyoid and branchial musculature of Urodela where the innervation does not harmonise with the position of the muscle—the innervation being held to be a clue to the derivation of the muscle elements. Göppert had expressed the same theory in the statement that a muscle never changes its innervation in the course of its phylogenetic development.) Drüner consequently described the muscle in most Urodela as a Transversus ventralis iv. As regards Necturus and Proteus, he stated that the muscle is homologous with Transversus ventralis iv of Salamandra and Triton in position and form, i.e. is a Transversus ventralis iv which has shifted forwards and become a Transversus ventralis iii. In Megalobatrachus max. the muscle has shifted forwards another segment and becomes a Transversus ventralis ii.

In regard to the corresponding Levatores arcuum, he stated that in Necturus and Proteus there is no demarcation possible between a Levator iii and a Levator iv, nor are there any remains of a gill-cleft. So that, unless it were proved by ontogeny that such existed, it is possible that a Levator iv, cartilage, and gill-cleft, have disappeared and that the insertion of the Levator into the inscriptio tendinea behind Ceratobranchiale iii is due solely to a caudal extension of Levator iii. In Megalobatrachus max. the Levator, which is inserted into Ceratobranchiale ii and the inscriptio tendinea behind it, may represent Levator ii, or ii and iii, or ii and iii and iv. Drüner, further, stated that there is evidence in Salamandra and Triton larvae of at least one branchial segment behind the fourth, between that and the Dorsolaryngeus. In Salamandra there is a short inscriptio tendinea extending backwards from Ceratobranchiale iv. Levator iv is separated into two portions, of which the anterior is inserted into Ceratobranchiale iv and the posterior into the inscriptio. The Transversalis ventralis is attached laterally, from before backwards, to (*a*) Ceratobranchiale iv, (*b*) the inscriptio, and (*c*) the ligamentum branchiopericardiacum. Between portions (*b*) and (*c*), i.e. behind the fourth branchial

arch there is, in young embryos (size not stated), an epithelial connection between the pharyngeal epithelium and the skin which represents a sixth gill-cleft. Again, on the left side of a 25 mm. Triton larva the Levator arcus iv consisted of two portions, inserted (*a*) into the cartilage, and (*b*) into the inscriptio extending back from it; whilst on the right side there was in addition a Levator v inserted at the junction of the inscriptio tendinea and the ligamentum branchio-pericardiacum. Between Levator iv and Levator v was an epithelial connection between the epithelium of the pharynx and the Plica omo-branchialis (which is formed from the fourth "Kiemenblättchen" and the skin of the shoulder region). This lies at the position where a sixth visceral-cleft would be expected and represents the remainder of it. The position agrees with that found in Salamandra larvae.

In Siredon Levator arcus iv is inserted to Ceratobranchiale iv and an inscriptio tendinea extending back from it. The Transversus ventralis arises from ceratobranchiale iv, the inscriptio and the ligamentum branchio-pectorale. Further, the fourth branchial nerve gave off an inconstant sensory branch which passed under the ligamentum branchio-pectorale, lying behind the position in which—on comparison with Salamandra and Triton larvae—the sixth gill-cleft is to be sought. This is a rudiment of a R. posttrematicus v. Once a small epithelial vesicle was found which was regarded as the remains of gill-cleft epithelium. Also a fine nerve was given off from the R. pharyngeus of the fourth branchial nerve, which was regarded as a R. pretrematicus vi.

There is thus in these larvae the remains of a sixth gill-cleft behind Ceratobranchiale iv, and the Transversus ventralis has fourth and fifth branchial elements. In Triton there is also a Levator v. The laryngeal structures—cartilage, Dilatator laryngis, and laryngeal muscles—consequently do not belong to a fifth branchial segment, as Wilder, Gegenbaur and Göppert supposed, but to some more posterior segment, at least to a sixth, possibly to one still further back.

Laryngo-tracheal skeleton

Anura. The laryngeal cartilages of Anuran larvae consist of a short rod on either side of the larynx. The adult conditions have been described by Henle and Wilder, and their development by Märtens.

Gymnophiona. Göppert has described the condition of the laryngeal cartilages in a late larva of Ichthyophis (*vide infra*).

Urodela. The laryngo-tracheal skeleton of Urodeles consists of a continuous or interrupted cartilaginous or fibro-cartilaginous rod on either side of the larynx and trachea[1].

[1] The pars trachealis cart. lat. is not present in Necturus where the short trachea is surrounded by fibrous tissue only; it is present in other Urodela, cartilaginous in Siredon, Salamandra, Triton, Ellipsoglossa and Proteus, fibro-cartilaginous with or without islands of cartilage in Menopoma, Megalobatrachus max., Amphiuma and Siren. It is continuous with the pars laryngea in Menopoma, Megalobatrachus max., Ellipsoglossa, Amphiuma, Siredon, Proteus and Siren. It is separated in Salamandra and Triton (Drüner).

Neither Henle (1839) nor Fischer (1864) discussed the derivation of these structures.

In 1892 similar, but not identical, theories were independently advanced by Wilder and Gegenbaur.

Wilder suggested that the pars laryngea is homologous with the fifth branchial arch of Selachians and the inferior pharyngeal bone of Teleostei, and for the following reasons: (1) Every form possesses either a fifth branchial arch or a laryngeal cartilage in the same location typographically. No animal possesses both. The sudden appearance of such well-developed hyaline structures as the laryngeal cartilages and the sudden disappearance of other well developed structures such as the fifth branchial arch are both unusual phenomena and when considered together may well point to the theory. (2) The fifth branchial arch in Selachians is supplied by X^4. "This same nerve follows the arytenoids and supplies this region throughout the vertebrate realm under the name of Ramus recurrens." (3) Another example of former branchial arches entering the service of the larynx is furnished by the thyroid cartilage, which develops from the second and third branchial arches (Dubois). Wilder also stated that in Triton the pars trachealis is developed from the connective tissue surrounding the trachea at a time when the pars laryngea is an already-developed hyaline structure, and regarded the laryngo-tracheal skeleton as derived from two sources—the pars laryngea from a fifth branchial arch, and the pars trachealis which is a new formation.

Gegenbaur suggested that the cartilago lateralis is homologous with the fifth branchial arch of fishes, and for the following reasons: (1) There is a similarity between the laryngeal muscles and the Mm. interarcuales ventrales of the branchial skeleton. The Transversus ventralis iv is to be compared with this musculature. (2) Amphibia show an atrophy of the branchial skeleton, increasing caudally. The cartilago lateralis has still more diminished in size and lost its union with the fourth bar—both phenomena have parallels in the branchial skeleton. (3) The fifth branchial bar of Selachii (other than Heptanchus and Hexanchus) shows signs of atrophy, and the inferior pharyngeal bone of Teleostei—which is derived from the fifth branchial arch—is a structure with many possibilities of modification. Wiedersheim (1886) had regarded the pars laryngea as the primitive portion of the laryngo-tracheal skeleton, to which the pars trachealis became secondarily united. Gegenbaur, however, found that in Salamandra larvae there is a continuous cartilage extending from larynx to bronchi, which subsequently separates into pars laryngea and tracheal skeleton. The earlier stage corresponds to that of adult Proteus and probably represents the ancestral condition.

Wilder, in 1896, abandoned his theory of an independent origin for the tracheal elements, and accepted that of Gegenbaur, as did also Göppert in 1894 and 1898.

Drüner (1901 and 1904) accepted the theory that the pars laryngea is

homologous with a branchial bar—not, however, with the fifth, but with either a sixth or a still more caudal one. This modification of Wilder's and Gegenbaur's theories was occasioned by the discovery of certain structures (*vide* pp. 129, 130) behind the fourth bar and its muscles, which, he held, represented at least one branchial segment between the fourth and that of the cartilago lateralis. He stated that the transitory continuity of the laryngo-tracheal skeleton in Salamandra is not present in Triton and Siredon where the tracheal portion develops independently in the form of many cartilaginous islands, and is no proof of a single derivation. It is paralleled by the transitory fusion of the various parts of the branchial skeleton. He consequently regarded the condition in Proteus (with a continuous laryngeal and tracheal skeleton) as rudimentary rather than primitive; and adhered to the earlier opinion of Wilder that the laryngeal and tracheal skeleton are distinct structures, and suggested that the latter might be either derived from one or more branchial bars behind the pars laryngea or be new formations.

The pars laryngea is not uniform in shape in Urodeles, and different opinions have been advanced as to which is the most primitive form. In Siredon and larvae of Triton and Salamandra it is a roundish rod-like structure. The Dilatator laryngis is inserted to it, the Laryngeus ventralis and the Laryngeus dorsalis when present[1] arise from the Dilatator laryngis by inscriptio tendinea. In Necturus and Proteus the pars laryngea, pointed in front, broadens to a flat plate, from the lateral edge of which a hook-like process projects backwards. The hind end of the process is tied to the inner limb of the plate by a ligament, which chondrifies in Proteus. The Dilatator laryngis is inserted to the lateral edge of the cartilaginous plate and the hook-like process, and the Laryngei dorsalis and ventralis arise from the upper and lower surfaces.

Göppert held that the form present in Necturus and Proteus is the more primitive and that of Siredon and larvae of Triton and Salamandra is secondary, owing to disappearance of the lateral part of the cartilage, with resulting shifting of the origins of the Laryngei dorsalis and ventralis to the tendons of the Dilatator laryngis. Drüner held the reverse opinion.

In Ellipsoglossa, Menopoma, Megalobatrachus max., and Amphiuma the pars laryngea has an oblique direction, from dorso-oral to ventro-caudal. The ventral ends meet and are tied together by connective tissue in the ventral median line (in Amphiuma by a cartilaginous bridge). The cartilage lies just beneath the mucous membrane and forms a support for the Rima glottidis which partially separates the laryngeal cavity into an anterior part—the vestibulum, and a posterior—the laryngo-tracheal cavity. In Menopoma and Megalobatrachus max., there is a processus trachealis projecting backwards from the pars laryngea close to the mid-dorsal line.

[1] The Laryngeus dorsalis arises from the tendon of the Dilatator laryngis in Triton, it is absent in Siredon, whilst in Salamandra larvae it was stated by Göppert to be absent, by Drüner to be present and to arise from the tendon of the Dilatator laryngis.

Drüner held that this form of the cartilage is secondary to that present in Salamandra, Triton and Siredon, and also that the processus trachealis is due to the fusion of tracheal elements with the pars laryngea.

A theory of the cartilago lateralis, absolutely different from that of the foregoing observers, was advanced by Wiedersheim (1904) from his investigations of the larynx in Ganoids and Dipnoi. He suggested, from analogy with Protopterus and Lepidosiren, that possibly the cartilago lateralis of Amphibia was primitively a tendon-chondrification without any phylogenetic relationship to the branchial bars.

Laryngeal muscles

Anura. Göppert (1894) described the laryngeal muscles of a 10 mm. larva of Rana as consisting of a s. Dilatator laryngis, Dorso-laryngeus and a Constrictor laryngis. The first named arises from the tissue lateral to the pharynx. He was of opinion, from comparison with Urodela, that the Dilatator laryngis had lost its constrictor action on the pharynx and become restricted in its action to the larynx. The Constrictor laryngis consists of a simple paired ring with median dorsal and ventral raphés, continuous ventrally with a Transversus ventralis iv. He concluded that it is homologous with the Laryngeus ventralis of Urodela. In 1898 he modified this opinion and advanced the theory that each half is homologous with the Laryngeus ventralis and the Laryngeus dorsalis of Urodela.

According to Wilder (1896) there is in the larva no Levator arcus branchialis iv, and at metamorphosis the Dilatator laryngis of the larva becomes separated into a (dorsal) Petro-hyoideus iv and a ventral Dilatator laryngis. According to Göppert (1894) a Levator arcus iv is present in the larva, and gains a new insertion into the processus postero-medialis at metamorphosis, forming the Petro-hyoidei posteriores or at least their hinder portion, and the only change in the Dilatator laryngis of the larva is that it gains an attachment to the processus postero-medialis.

Gymnophiona. The laryngeal muscles of a late larva of Ichthyophis were described by Göppert (1894) *vide infra.*

Urodela. Fischer (1864) included the Dilatator laryngis and Transversus ventralis iv in the muscle-system of a Constrictor laryngis, which appeared to be a repetition of the Levatores arcuum.

Wilder (1892) regarded the Dilatator laryngis as homologous with the dorsal segment of the fifth branchial arch of Selachii.

Göppert (1894) regarded the Dilatator laryngis as a Levator arcus v serially homologous with the Levatores of the branchial arches. This opinion was accepted by Wilder (1896).

Drüner also regarded the Dilatator laryngis as serially homologous with the Levatores arcuum, though of some segment behind the fifth branchial (*vide supra*).

Wilder (1892) put forward the theory that the laryngeal ring of muscle is a continuation of the ring musculature of the alimentary canal which the

developing respiratory tract carried with it when it arose as a diverticulum of the former. Its first action was that of a sphincter and it gained relations to the pars laryngea later.

Göppert (1894) argued, against Wilder's theory, that there is a fundamental difference between smooth and cross-striped muscle-cells; the former are single cells, whilst the latter form a syncytium, and the relationship of the two kinds of cells to nervous centres is quite different. In Siredon, ontogenetically, the Laryngeus ventralis is a derivative of the Transversus ventralis iv; and in Triton larvae, although there is no direct proof of the origin of the Laryngeus dorsalis, yet it stands in the closest relationship to the Dilatator laryngis.

Wilder (1896) abandoned his theory of 1892, and homologised the "intrinsic laryngeal muscles" (i.e. Laryngei and Constrictor) with a Transversus ventralis v, which has become separated into dorsal and ventral portions by the growth and flattening out of the arytenoids—the homologues of the fifth branchial bars.

Göppert (1898) abandoned his theory of 1894 that the Laryngeus ventralis is derived from the Transversus ventralis iv, and stated that they are serially homologous, the Laryngeus ventralis being the Transversus ventralis of a fifth branchial branch and homologous with the Transversus ventralis v of Acipenser and the Transversus ventralis posterior of Amia. The Laryngeus dorsalis is possibly derived from the same source.

Drüner (1901 and 1904) was of opinion that the Laryngei and Constrictor are homologous with a Transversus ventralis vi, or possibly with that of a still more posterior segment which has migrated forwards to that of the Dilatator laryngis and Arytenoid. The grounds for this opinion were derived from its innervation. The Dilatator laryngis is innervated in all cases from the N. intestino-accessorius X (with the addition, in Amphiuma and Siren, of branches from the N. recurrens, and in Menopoma of a fine twig from the nerve to the fourth branchial arch). On the other hand, the Laryngei and Constrictor are innervated by the N. recurrens intestinalis X. The N. recurrens intestinalis X is thus a collecting nerve in which the elements of at least two, perhaps more, branchial segments are included, and of these at least one is to be reckoned as being behind the segment of the Dilatator laryngis.

These observers have advanced various theories as to the primitive form of the intrinsic laryngeal muscles in Urodela.

Wilder (1892) considered as typical the condition present in Siren and Menopoma where the larynx is surrounded by a complete muscle-ring and the arytenoids are partly enclosed by it and partly lie in its substance. In 1896, after publication of Göppert's 1894 paper, he stated "I hardly feel like considering the Sphincter of Salamandridae as more than a modification of the original Laryngei and of thus considering the laryngeal ring of Triton as essentially different from that of Siren or of Necturus."

Göppert (1894) was of opinion that the primitive Urodelan condition is

shown by Necturus and Proteus, where there are only Laryngei, attached to a broad arytenoid, and that the Caducibranchiata (other than Amphiuma), with a Constrictor and Laryngei attached to the tendon of the Dilatator laryngis, represent a derivative condition due to a diminution in breadth of the arytenoid. This was supported by observations on Siredon (in which no Laryngeus dorsalis is found). In 13·5 mm. specimens he found a great number of young muscle-elements dorsal to the already formed Laryngeus ventralis, and in 18 mm. specimens the primordium of the Constrictor was represented by a small bundle of young muscle-elements dorsal to the Laryngeus ventralis with its median end spreading towards the dorsal median line of the larynx. Similarly, in 10 mm. larvae of Triton alpestris he found the Constrictor being proliferated from the Laryngeus ventralis. In 1898 he modified this opinion as regards Triton saying that he could now not exclude the Laryngeus dorsalis from taking part in the formation of the Constrictor, and that the method followed in Siredon was due to the absence of a Laryngeus dorsalis.

Göppert regarded the Constrictor of Amphiuma as due to the lateral union on each side of a Laryngeus dorsalis and ventralis.

Drüner regarded the condition of Siredon, Salamandra, and Triton—with Laryngei and Constrictor—as the primitive one, and that of Necturus and Proteus—with Laryngei only—as secondary. Further, Wilder had stated that, in Necturus, the first and last sections of a transverse series show continuous fibres of a circular outline entirely enclosing the Laryngei and acting as a Constrictor, and Drüner stated that in one case of Proteus he found the rudiment of a Constrictor on one side.

OBSERVATIONS

Ventral branchial muscles

Anura. In a 7 mm. larva of Rana temp. there are four branchial muscle-plates. That in the first branchial segment (fig. 1) has separated from the pericardium and consists, from below upwards, of the primordia of the Subarcualis rectus i, Marginalis i, and Levator i. The second, third and fourth branchial muscle plates (figs. 2, 3) are continuous, ventrally, with the pericardial wall. The fourth lies slightly posterior to the sixth gill-cleft.

In a 7½ mm. larva the second, third and fourth branchial muscle plates have separated from the pericardial wall. From the ventral ends of the second and third, Subarcuales recti ii and iii have separated off. From the ventral end of the fourth (figs. 5 and 6) Subarcualis rectus iv has separated off and the (rudimentary) Transversus ventralis iv passes ventro-medially. Each Subarcualis rectus extends forwards into the next segment.

In an 8 mm. larva Subarcuales recti i and ii have fused together forming a muscle passing from Branchiale ii to the Hyale. The Transversus ventralis iv (figs. 8, 9, 10) is better marked, passing towards the ventral aspect of the laryngeal groove.

In an 11 mm. larva (fig. 11) a muscle, passing from Branchiale i to the Hyale, has separated from the forepart of the muscle passing from Branchiale ii to the Hyale. The Subarcuales recti iii and iv have nearly fused together (fig. 12), and, in a 12 mm. larva, form a muscle passing from Branchiale iv to Branchiale ii. The Transversus ventralis iv has disappeared.

It is observable that the fourth branchial muscle-plate, before separation from the pericardium, shifts a little backward so as to lie posterior to the (rudimentary) sixth gill-cleft, and, when the fourth branchial bar becomes formed in an 8 mm. larva, it passes backwards external and posterior to the sixth gill-cleft.

Transversus ventralis iv is rudimentary and disappears early; it never forms an independent muscle passing from Branchiale iv to the middle line. It is also absent in larvae, of lengths from 10 to 12 mm. of Bufo lentig., Alytes, and Pelobates.

Gymnophiona. The development of the ventral branchial muscles has not yet been traced, but Fischer, Wiedersheim, Fürbringer and Göppert have partially described them.

In 3·5 and 5·9 cm. larvae of Ichthyophis (figs. 23–25) all four branchial bars are present, the third and fourth being fused at their ventral ends. Copula i, s. Basihyale and Copula ii, s. Basibranchiale i are present. Subarcuales recti iv, iii, ii and i are present, each passing from its branchial bar to the next anterior one. The foremost—Subarcualis rectus i—is broader than those behind, and, as it passes forward, divides into two portions, the inner of which is inserted into the Hyale, whilst the outer is prolonged in front of the Hyale and is inserted into the lateral edge of the Basihyale.

In a 7 cm. larva of Siphonops (figs. 26–31) the third and fourth branchial bars are fused, except at their dorsal ends, and there is no Basihyale. Subarcualis rectus iv is absent. Subarcuales recti iii, ii and i are present. i is single and inserted anteriorly into the Hyale. In the adult stage Subarcualis rectus i persists, whilst ii and iii have degenerated into tendons.

The adult stages of Caecilia palmiri and Hypogeophis are similar to the adult stage of Siphonops.

A Transversus ventralis i (not hitherto described) is present in larvae of Siphonops and Ichthyophis. In the former (figs. 26 and 27) its lateral end is attached to Branchiale i and its median end to a short transverse aponeurosis which connects it to its fellow. In Ichthyophis (fig. 24) its lateral end is attached to Subarcualis rectis i, and its median end partially to Copula ii and partially to a median raphé. The muscle is absent in the adult stages of Siphonops, Caecilia palmiri and Hypogeophis.

There are no Transversi ventrales ii and iii in the larval stages of Siphonops and Ichthyophis.

Transversus ventralis iv has been described by Göppert, in a late larva of Ichthyophis, as arising by two heads from the fused third and fourth branchial bars and passing to an aponeurosis ventral to the trachea. In the younger

larvae investigated I find that both heads arise from the fourth bar. In a 7 cm. larva of Siphonops the muscle arises from the nearly completely fused third and fourth branchial bars by a single head.

The differences in the form of Subarcualis rectus i between Ichthyophis and Siphonops are related to the presence in the former and absence in the latter of Copula i s. Basihyale. The absence of a Subarcualis rectus iv in Siphonops may be secondary and related to the greater degree of fusion of the third and fourth branchial bars.

Urodela. In Menopoma seven gill-clefts are developed, and correspondingly there are five branchial segments. In a larva of 15 mm. (figs. 33, 34) the sixth and seventh gill-clefts cannot be distinguished from each other; they form a lateral projection, with a slit-like lumen, of the branchial endoderm, 140μ long, which reaches the ectoderm. In a larva of 17 mm. (fig. 37) the projection is 160μ long, and on its ventral surface is a slight bulge, the first indication of the seventh gill-cleft. In a larva of 19 mm. the sixth gill-cleft has disappeared on the right side, leaving no trace, whilst on the left side the anterior end of the sixth gill-cleft persists as an epithelial plug or stump continuous with the branchial endoderm (fig. 43). Behind this, the seventh gill-cleft reaches the ectoderm, on both sides (fig. 44). The distance between the anterior end of the fourth and that of the fifth gill-cleft is 170μ. On the right side the distance between the anterior end of the fifth and that of the seventh gill-cleft is 280μ; on the left side the distance between the anterior end of the fifth gill-cleft and the stump of the sixth is 180μ, and the distance between that and the anterior edge of the seventh gill-cleft is 110μ. The length of the third branchial segment (between the fourth and fifth gill-clefts) is thus 170μ, that of the fourth branchial segment is 180μ, that of the fifth branchial segment is 110μ. The fifth branchial segment, which does not contain any branchial muscle-plate, or branchial bar, or branchial aortic arch, is thus shorter than the more anterior ones.

The seventh gill-cleft, which does not perforate, is present in larvae in this stage up to one of 22 mm.; it has disappeared in larvae of 24 mm. without leaving any trace. The stump of the sixth gill-cleft on the left side persists in larvae up to the length of 28 mm. In one of 32 mm. it has become detached from the endoderm.

Four branchial muscle plates are developed, in the first four branchial segments. In a larva of 15 mm. (figs. 32, 33) those in the first three segments have become detached from the pericardial epithelium, whilst that of the fourth branchial segment is still continuous with it. The primordium of the hypobranchial spinal muscles forms a continuous column, and extends as far forwards as the hyoid segment. In a larva of 17 mm. (fig. 36) the fourth branchial muscle-plate has also become detached from the pericardial epithelium. These muscle plates lie lateral to the branchial bars, which have begun to develop. The ventral portions of the branchial muscle-plates form the Subarcuales, and, in the fourth branchial segment, the Transversus ventralis as well. The primordium of the hypobranchial spinal muscles has

extended forwards to Meckel's cartilage and separated into Genio-hyoid and Sterno-hyoid. The hind end of the Genio-hyoid has grown backwards a little, ventral to the Sterno-hyoid. In a larva of 18 mm. (fig. 38) (in which the sixth gill-cleft is still continuous with the ectoderm) the Subarcualis rectus iv has begun to grow forward. Its hind end is continuous with the lateral end of the Transversus ventralis iv which has begun to grow transversely inwards (fig. 39). In a larva of 19 mm. Subarcualis rectus i has grown forwards to the second gill-cleft, Subarcuales obliqui ii and iii have grown forwards and downwards and meet, laterally to the Sterno-hyoid (fig. 42). The fourth branchial bar now passes from the fourth branchial segment backwards, outside the stump of the sixth gill-cleft on the left side, into the fifth branchial segment, and then upwards; i.e. on the total or partial atrophy of the sixth gill-cleft it bulges backwards into the fifth branchial segment (figs. 43, 44). Correspondingly, the hind end of the Subarcualis rectus iv and the lateral end of the Transversus ventralis iv have shifted back into the fifth branchial segment (figs. 43, 44). The front end of Subarcualis rectus iv has grown forwards into the second branchial segment. The Transversus ventralis iv has now further developed, and passes transversely inwards to the middle line, on the left side under, and behind, the stump of the sixth gill-cleft. In a larva of 22 mm. the Urobranchiale has developed (see later, p. 141), and the hind end of the Genio-hyoid has grown further back. In a larva of 24 mm., where the seventh gill-cleft has disappeared, the hind end of Subarcualis rectus iv and the lateral end of Transversus ventralis iv are relatively further back, with the result that the anterior edge of Transversus ventralis iv is oblique and lies, on the left side, posterior to the stump of the sixth gill-cleft (figs. 48, 49). The anterior end of Subarcualis rectus iv (*a*) reaches the first branchial bar, whilst off-shoots (*b* and *c*) are given off to the second and third branchial bars (fig. 51). The Subarcuales obliqui ii and iii unite and pass to the sheath of the Sterno-hyoid.

There is little further change in the Subarcuales; in a 32 mm. larva the ventral end of the second gill-cleft is shallower and the anterior end of Subarcualis rectus i is attached to the Ceratohyale. Transversus ventralis iv gradually spreads backwards, forming a broad sheet; in a 34 mm. larva its posterior edge underlies the Laryngeus ventralis. In the adult (Drüner) the muscle underlies the trachea.

Miss Platt (1897) stated that in Necturus Subarcualis rectus i is developed from the ventral end of the mesothelial tissue of the glosso-pharyngeal arch. Subarcualis obliquus ii grows forwards from the mesothelium of the first vagus arch near the point where this tissue joins the wall of the pericardium. Subarcualis iii (*a* and *b*) arises as a single muscle from the wall of the pericardium in the region where the mesothelium of the second vagus arch unites with the pericardial wall.

She did not mention the Transversus ventralis iii, nor state how many gill-clefts are developed, but the figures given show five.

My observations in regard to the Subarcuales of the first two branchial

arches coincide with those above stated, but they are a little different in regard to the number of gill-clefts and the development of the third branchial muscle-plate.

In a larva of 12 mm. there are five gill-clefts—the sixth not being yet developed. In a larva of 13 mm. the fifth gill-clefts are reduced to stumps attached to the endoderm, on both sides, and the sixth gill-clefts have developed and reach the ectoderm. The length of the third branchial segment (between the fourth and fifth gill-clefts) is 120μ, that of the fourth is 90μ. In a larva of 15 mm. the sixth gill-clefts have disappeared leaving no trace. In a larva of 18 mm. the stumps of the fifth gill-clefts have separated from the endoderm, and in one of 20 mm. the right one has disappeared.

In the larva of 12 mm. (fig. 57) the third branchial muscle-plate is continuous ventrally with the epithelium of the pericardium. In a larva of 13 mm. (figs. 60 and 61) the third branchial bar passes backward from the third branchial segment lateral to the stump of the fifth branchial cleft into the fourth branchial segment and then upward. The third branchial muscle-plate has separated from the endoderm, and its ventral end has developed into the Subarcualis rectus iii and the Transversus ventralis iii. The former grows forward from the fourth branchial segment laterally to the stump of the fifth gill-cleft, the latter passes inwards, partly under the stump of the fifth gill-cleft (fig. 60), and partly behind it (fig. 61). In the larva of 16 mm. (figs. 67, 68), where the sixth gill-clefts have disappeared, the hind end of the Subarcualis rectus iii and the lateral end of Transversus ventralis iii are still further back, so that the front edge of Transversus ventralis iii is behind the stump of the fifth gill-cleft.

Morphology of the ventral branchial muscles

Subarcuales. Anura. In larvae of Rana the Subarcuales recti are simple. The only secondary changes are (1) Fusion of Subarcuales recti i and ii to form a long muscle, and the subsequent separation of a slip from its anterior half to form a muscle passing from the first branchial to the hyoid bar. (2) The fusion of Subarcuales recti iii and iv to form a long muscle. The resulting condition is also present in larvae of Bufo, Alytes, and Pelobates. The condition of the Subarcuales in larvae of Aglossa has not yet been described.

Gymnophiona. The ventral branchial muscles in Siphonops and Ichthyophis have been described above (page 136). These are the only larval forms yet investigated.

Urodela. Subarcualis rectus i, as shown by Drüner, passes from the first branchial bar, generally from Ceratobranchiale i to the Ceratohyale. In all the larvae examined it was found that a delay occurs in the attachment of the anterior end of the muscle to the Ceratohyale, it is for a time inserted into the epithelium of the ventral end of the second gill-cleft, which forms a groove in the floor of the branchial region, e.g. Menopoma (fig. 51). The Subarcuales obliqui have been described by Fischer and Drüner. The latter

states that in Ellipsoglossa (adult), Megalobatrachus max. (adult), Siredon, Menopoma (adult), Salamandra and Triton larvae, the muscles pass forwards and downwards, unite by their bellies or tendons, and are inserted into the fascia of either the Rectus profundus or superficialis, and so act on the Urobranchiale.

Two exceptions to this general rule are described by Drüner. He stated that in Necturus and Proteus (with only three branchial bars) only one muscle —Subarcualis obliquus ii—is present, and that this, in Proteus, is inserted on the fascia of the Rectus profundus, but in Necturus is inserted into Hypobranchiale i, i.e. in the latter is a Subarcualis rectus ii. In numerous embryos, however, I find the muscle inserted into the fascia of the Rectus profundus (fig. 66), i.e. it is a true Subarcualis obliquus ii. The other exception is that of Amphiuma (adult), where Drüner stated that only one Subarcualis obliquus is present, passing from Ceratobranchiale iii to Branchiale i and not to the fascia of the Rectus.

I find that in Menopoma (larva) and Ellipsoglossa (larva) the common tendon of Subarcuales obliqui ii and iii is inserted partly into the sheath of the Rectus profundus and partly into the Urobranchiale.

The above can be summarised as follows: In Urodela, with exception of Amphiuma (adult form), the Subarcuales of the second and third branchial bars (or, in the case of Necturus and Proteus, that of the second bar) do not grow forward to the next anterior bar, as in Anuran and Gymnophionan larvae, but forward and downward, becoming Subarcuales obliqui, joining together and passing into a tendon which has direct or indirect relations to the Urobranchiale.

A Urobranchiale, either continuous with the branchial skeleton or as a separate structure, has been described by Drüner in all the Urodela he examined, with exception of Menopoma (adult), Megalobatrachus max. (adult), Amphiuma (adult), and Ellipsoglossa (adult). In the larvae of Menopoma and Ellipsoglossa, however, a Urobranchiale is present, as a structure either separate or continuous with the branchial skeleton. In these two forms, therefore, the Urobranchiale disappears at metamorphosis or earlier (it has already degenerated in a 40 mm. Menopoma), and this may also be the case in Megalobatrachus max. and Amphiuma[1], for its development appears to be related to the overlapping of the anterior end of the Sternohyoid s. Rectus cervicis by the Geniohyoid—which is universal in Urodela. This overlapping is due to a backward growth of the hind end of the Geniohyoid ventral to the Sternohyoideus s. Rectus cervicis.

The development of the Urobranchiale is not uniform in Urodela. Stöhr (1880) described it in Triton as due to division into dorsal and ventral portions of an original primordium connecting together the median ends of the hyoid and first two branchial bars. Miss Platt (1897) described a second Basi-

[1] In 45 mm. larvae of Amphiuma (Hay) the second Basibranchiale and Urobranchiale are both absent.

branchiale in Necturus as developing from cells on the anterior wall of the pericardium. She inclined to regard it as a foreign element associated secondarily with the branchial arches. Gaupp (1905) pointed out the homology of this "second Basibranchiale" of Necturus with the Urobranchiale of Salamandridae larvae, but added that it was not yet shown whether it represents an independent Basibranchiale, which in Salamandridae larvae develops in concrescence with the anterior Basibranchiale.

I find that the hyobranchial skeleton of a 12 mm. larva of Ellipsoglossa (figs. 71 and 72) is in a precartilaginous condition. The median ends of the hyoid and first and second branchial bars are continuous ventrally with a median rod which represents the first and second Basibranchialia. The Urobranchiale is a ventral process of the second Basibranchiale. In a 15 mm. larva (figs. 73–76) chondrification has taken place; the Urobranchiale has extended ventro-posteriorly, and the attachment of the second branchial bars has spread along it.

The development of the Urobranchiale in Triton, Salamandra, and Amblystoma, is similar to that in Ellipsoglossa.

In a 20 mm. larva of Menopoma (fig. 46) the Urobranchiale is a ventro-posterior process of the precartilaginous second Basibranchiale. It has separated from the second Basibranchiale in a 22 mm. larva, and is chondrified as a separate structure in a 32 mm. larva (figs. 53 and 54). This condition persists in a 36 mm. larva. In a larva of 40 mm. it has degenerated into a small clump of cells. In the adult it is absent (Drüner).

In Necturus no second Basibranchiale is developed. In an embryo of 16 mm. (figs. 64–66) the Urobranchiale is a precartilaginous rod passing ventro-posteriorly from its junction with the ventral ends of the first branchial bars.

The Urobranchiale may thus be developed (1) as a ventro-posterior process of the second Basibranchiale (Ellipsoglossa, Triton, Salamandra, Amblystoma), (2) as a ventro-posterior process of the second Basibranchiale which separates off and subsequently chondrifies (Menopoma), (3) as a structure passing ventro-posteriorly from the ventral ends of the first branchial bars, no second Basibranchiale being present (Necturus).

The attachment of the ventral end of the first branchial bar extends along the Urobranchiale in Ellipsoglossa, Triton, Salamandra, and Amblystoma, but does not do so in Necturus.

These phenomena suggest that some ancestral Urodelan stock possessed a Urobranchiale as a ventral process of the second Basibranchiale, with no extension of the ventral end of the first branchial bar along it—i.e. a condition very like that of a 12 mm. Ellipsoglossa or 20 mm. Menopoma.

Subarcualis rectus iv has been described by Fischer and Drüner. The latter states that it is present in the larval stages of Siredon, Salamandra and Triton, and in the adult stages of Amphiuma and Menopoma: but is absent in the adult stages of Siredon, Salamandra, Triton, Megalobatrachus max. and

Ellipsoglossa. My observations show that it is also present in the larval stages of Ellipsoglossa and Menopoma.

It is a muscle that takes origin from the fourth branchial bar, passes forward and separates into three slips (*a*, *b*, *c*) which are attached respectively to the first, second and third branchial bars. In Siren only (*a*) is present. In Necturus and Proteus there is a similar Subarcualis rectus iii which takes origin from the third branchial bar, and is attached, (*a*) to the first, and (*b*) to the second, branchial bar.

The forward extension of Subarcualis rectus iv in front of the third branchial bar—to the second and first bars—is related to the secondary function and position of Subarcuales ii and iii. (It is noticeable that this secondary form of Subarcualis rectus iv also exists in Amphiuma (adult), and that in Megalobatrachus max. (adult, with only two branchial bars) though no Subarcualis rectus iv is present yet Subarcuales obliqui ii and iii and not Subarcuales recti ii and iii are present (*vide* Drüner). These facts form additional evidence in favour of the theory, suggested above, that a Urobranchiale exists in the larval forms of these Urodela also.)

There are thus five closely related phenomena in Urodela. (1) Backward growth of the hind end of the Genio-hyoid ventral to the forepart of the Rectus cervicis. (2) Formation of a Urobranchiale. (3) Formation of Subarcuales obliqui ii and iii (Subarcualis obliquus ii in Necturus and Proteus). (4) Forward extension of Subarcualis rectus iv (Subarcualis rectus iii in Necturus and Proteus) to the first branchial bar. (5) Separation of a superficial, ventral, portion of the Rectus cervicis, attached to the Urobranchiale.

No one of these secondary phenomena occur in Anuran and Gymnophionan larvae, where the conditions are more primitive. (There is a small overlap of the Genio-hyoid and Rectus cervicis in Rana temp. larvae, but it is due to a backward extension of the former along the hypobranchial plate, and so of a different character from that of Urodela. The anterior end of the Rectus becomes attached to the Crista hyoidea (of Schultze), but this, as shown by Gaupp, is a ventral process of Basibranchiale i, and so not homologous with the Urobranchiale of Urodela.)

Transversi ventrales. Transversus ventralis i is present in larvae of Ichthyophis and Siphonops, but not in Anuran or Urodelan larvae. Transversus ventralis ii is not found in any Amphibia. Transversus ventralis iii is present in Necturus, and probably in Proteus, but not in other Amphibia. Transversus ventralis iv is present in larvae of Anura, Gymnophiona, and Urodela with four branchial bars. In Rana the muscle is rudimentary and soon disappears. In Ichthyophis it is attached to the fourth branchial bar, and, on the fusion of this with the third, to the fused bar, by two heads in Ichthyophis, by one in Siphonops.

In Menopoma, at the stage when the sixth gill-cleft reaches the ectoderm, the ventral end of the fourth branchial muscle-plate (attached to the pericardial wall) and the primordium of the fourth branchial bar are in front of

it and do not extend outside or behind it. When the gill-cleft is reduced to a stump, the fourth branchial bar passes outwards and backwards laterally to the stump, then upwards and posterior to it, and correspondingly the primordia of the Subarcualis rectus iv and Transversus ventralis iv have migrated posterior to the stump, and from this point grow forwards and inwards respectively.

The whole series of events is due to an enlargement of the "branchial basket," whereby all the structures of the fourth branchial segment bulge backwards behind the stump of the sixth gill-cleft.

A similar series of events is observable in Rana, where—the sixth gill-cleft being never more than a stump—it occurs relatively earlier, before the ventral end of the fourth branchial muscle-plate separates from the pericardial wall.

In Necturus a similar series of events occurs in regard to the third branchial muscle-plate and the fifth gill-cleft. Only one Transversus ventralis is formed, i.e. the third. Transversus ventralis iii or iv subsequently extends backwards forming a broad sheet which underlies, to a variable extent, the respiratory tract (*vide* p. 128).

The above mentioned developments of Transversi ventrales may be tabulated as follows:

	1st	2nd	3rd	4th branchial segment
Gymnophiona, larvae	×	0	0	×
Anura, larvae	0	0	0	×
Necturus and Proteus	0	0	×	0
Urodela with 4 branchial bars ...	0	0	0	×

The theory of Wilder (*vide supra*, p. 128) is supported by these facts. It has to be remarked, however, that the Intermandibularis and Interhyoideus are probably not serially homologous with the Transversi ventrales of the branchial segments; and, further, that the phenomena in Necturus and Proteus possibly admit of an explanation other than that of the persistence of an ancestral feature which is lost in other Amphibia (*vide infra*, p. 147). His theory, then, should be limited to the branchial region, and restated as follows: primitively in Amphibia there was a series of ventral transverse muscles attached to the branchial bars.

The occurrence of Transversi ventrales ii, iii and v in Ceratodus may be adduced as additional evidence in favour of the theory.

Summary of the characteristics of the ventral branchial muscles

The Subarcuales are developed by forward growth of the ventral ends of the branchial muscle-plates.

In some primitive ancestral stock they probably formed a series of longitudinal muscles, the Subarcuales each passing from its branchial bar to the next in front.

In Anuran and Gymnophionan larvae few modifications occur. In Anuran larvae Subarcuales recti i and ii unite, forming one muscle, and subsequently

a lateral portion is separated from the anterior part and passes from the Branchiale i to the Hyale; and Subarcuales recti iii and iv unite forming one muscle. As regards Gymnophiona, in Siphonops larvae, where there is no Basihyale, Subarcualis rectus i is single, whereas in Ichthyophis larvae, where a Basihyale is present, Subarcualis rectus i separates into two muscles. In Urodela, whilst Subarcualis rectus i remains single, considerable modifications occur in the hinder subarcuales—probably associated with the backward growth of the Genio-hyoid and the formation of a Urobranchiale. These changes are, shortly, an insertion of Subarcuales ii and iii to the Urobranchiale directly or indirectly, so that they form Subarcuales obliqui ii and iii (in Necturus and Proteus ii only), and an extension forwards of the hindmost Subarcualis rectus (fourth in Urodela with four branchial bars, third in Necturus and Proteus) to Branchiale i.

Transversi ventrales are formed by ingrowth from the ventral ends of the branchial muscle-plates. Transversus ventralis i is present only in Gymnophionan larvae. Transversus ventralis iv (iii in Necturus and Proteus) is formed in all Amphibian groups, though it is rudimentary and soon disappears in Anuran larvae; it spreads backwards, forming a broad sheet, which in part or wholly underlies the respiratory tract.

Innervation of the ventral branchial muscles

Anura. The account given by Strong is not detailed, but he states that the Recurrens does not spread into the branchial region.

Gymnophiona. Norris and Hughes state that in Herpele (adult) the Recurrens innervates the Transversus ventralis iv in addition to the laryngeal muscles. In a 7 cm. larva of Siphonops, and in 3·5 and 5·9 cm. larvae of Ichthyophis I find that the Recurrens innervates the same muscles as in Herpele, i.e. it does not extend into the branchial region nor does it innervate the Subarcuales recti and Transversus ventralis i.

Urodela. Drüner stated that Subarcualis rectus i is innervated solely by the ix in Menopoma, Megalobatrachus max., and Necturus. It has an additional nerve supply from the hinder branchial nerve or nerves and the Recurrens intestinalis in other Urodeles. Subarcualis obliquus ii in Necturus is innervated by the second branchial nerve, in Proteus by this and probably also by the Recurrens. Subarcuales obliqui ii and iii in Ellipsoglossa and Menopoma are innervated by the second and third branchial nerves, in Megalobatrachus max. and Siredon by these and the Recurrens, in Salamandra and Triton by the Recurrens, in Siren ii by the second branchial nerve and iii by the Recurrens. In Amphiuma the single Obliquus is innervated by the second branchial nerve and the Recurrens.

Subarcualis rectus iv is absent in the adult forms of Ellipsoglossa, Megalobatrachus max., Siredon, Salamandra and Triton; in Menopoma (adult) *a* and *b* are innervated by the second and third branchial nerves, *c* by the fourth branchial nerve and the Recurrens; in Siredon (adult), Amphiuma (adult),

Salamandra and Triton larvae, *a* is innervated by the second branchial nerve and the Recurrens, *b* by the third branchial nerve and the Recurrens, *c* by the Recurrens; in Siren *a* (the only one present) is innervated by the second branchial nerve and the Recurrens. Transversus ventralis iii of Necturus and Proteus, and Transversus ventralis iv of other Urodeles, are innervated by the Recurrens. Drüner, as stated above p. 129, inferred from these facts that the Transversus ventralis iii or iv had migrated forward into the branchial region, and that a similar though less marked migration had taken place in the muscle-elements of the Subarcuales. Norris, holding with Drüner that the nerves are the most conservative structures in the branchial region, and "will thus constitute more reliable guides in the search for the primitive relations in this region than will the branchial arches themselves," states that there is "a considerable usurpation by the Ramus intestino-recurrens of territory of the ventral branchial region belonging originally to the post-trematic rami of the branchial nerves."

It is doubtful whether this statement implies a forward migration of muscle-elements, as Drüner thought; or a forward extension of nerve-fibres, the muscle-elements remaining constant.

But, however that may be, the phenomena of development show that the Transversus ventralis iv and the Subarcuales are developed from the ventral ends of the branchial muscle-plates.

It may be inferred that the ventral branchial muscles are more conservative than are their nerves.

Three processes appear to have occurred. (1) A disappearance of the ventral motor branches of the branchial nerves, in increasing degree from before backwards. (2) An additional or supplanting innervation by the Recurrens. (3) In the case of the Subarcualis rectus iv an innervation by the nerves of the branchial arches into which it grows—thus, in Menopoma, Subarcualis rectus iv (*a*)—which grows forward to the first branchial bar—is innervated by the second branchial nerve, (*b*)—which grows forward to the second branchial bar—by the third branchial nerve, (*c*)—which grows forward to the third branchial bar—by the fourth branchial nerve and the Recurrens.

Comparison of the innervation of the ventral muscles of the branchial bars in Anuran, Gymnophionan and Urodelan larvae shows that the secondary —additional or supplanting—innervation by the Recurrens intestinalis has been developed within the Amphibian phylum, and to the greatest extent in Urodela.

On the number of branchial bars and related muscles in Amphibia

Maurer (1902) described five gill-clefts and a post branchial body in Amphibia, and Drüner (1901) (*vide supra*, pp. 129, 130) six gill-clefts. Kingsley[1],

[1] Kingsley names the clefts: (*a*) hyomandibular, (*b*) the first branchial, (*c*) the second branchial, (*d*) the third branchial, in front of the fourth cartilaginous gill-arch, and then two pits behind this arch—these, according to his statement are the fifth and sixth—according to the reckoning adopted here, the sixth and seventh gill-clefts.

however, had stated (1892) that in an embryo Amphiuma (size not stated) there were two pits behind the fourth cartilaginous gill-arch, i.e. five branchial segments. Marcus (1908) stated that in larvae of Hypogeophis seven gill-clefts are developed (*vide infra*, p. 149), i.e. five branchial segments.

In Menopoma and Ellipsoglossa seven gill-clefts are developed, the last two behind the fourth branchial bar and its muscles. No muscle-plate or cartilaginous bar is developed in this fifth branchial segment.

The sum of this evidence suggests that five branchial bars with related muscles existed in Amphibian ancestors, but that the fifth disappeared long ago.

Drüner (*vide supra*, pp. 129, 130) came to the conclusion that Urodeles originally possessed a greater number of branchial arches than four. The evidence merits discussion. As regards the nerves found by him, it is possible that they have relation solely to the sixth and seventh gill-clefts. As regards the muscles, the phenomena of development do not bear out the theory that the stump of the sixth gill-cleft separates a Transversus ventralis iv from a Transversus ventralis v. Thus in Menopoma there is only one primordium developed—that of Transversus iv. This, at first, lies solely in the fourth branchial segment, then under the stump of the sixth gill-cleft, then posterior to it. The variation is due to the fact that, on the partial atrophy of the sixth gill-cleft, the Transversus iv, the hind end of Subarcualis rectus iv, and the fourth branchial bar, migrate into the fifth branchial segment; and, on the atrophy of the seventh gill-cleft, still further back. There is a similar progressive variation of the Transversus iv in relation to the sixth gill-cleft in Ellipsoglossa, and of Transversus iii in relation to the fifth gill-cleft in Necturus. The evidence, as regards muscle elements, is thus limited to the discovery of a Levator arcus v on one side in one larva of Triton. I have not seen this, however, in the many larvae of Menopoma, Ellipsoglossa, and Triton crist. I have examined.

It is probable, therefore, that the case described by Drüner is an instance of fluctuation, possibly of atavistic fluctuation, from the usual number of four branchial bars and related muscles in Urodela.

In support of these conclusions, it may be added that in Lysorophus—a member of the ancestral Urodeles, from the Pennsylvanian deposits—Sollas found only four branchial bars, the first three consisting of cerato-branchial and epibranchial elements, and the fourth of a train of fragments.

The case of Necturus, with only three branchial bars and related muscles, probably comes under a different category. All Amphibia, with exception of Megalobatrachus max. (adult), Necturus and Proteus, have four branchial bars and related muscles. Megalobatrachus max. has two branchial bars in the adult state (Drüner), but only the early stages of larval development have been published hitherto—by de Lange. In Necturus the development, described above, permits of comparison with Menopoma.

In Menopoma seven gill-clefts are formed, all of which reach the ectoderm.

The sixth disappears on the right side, whilst on the left side it forms an epithelial stump continuous with the endoderm. This becomes detached later on. The seventh disappears on both sides, without leaving any remnant. The fourth (and last) branchial muscle-plate lies, at first, anterior to the sixth gill-cleft. No muscle-plate is developed in the fifth branchial segment.

In Necturus six gill-clefts are formed, all of which reach the ectoderm. The fifth become detached from the ectoderm on both sides and form epithelial stumps continuous with the endoderm. They become detached later on. The sixth gill-clefts disappear on both sides and leave no trace. The third (and last) branchial muscle-plate lies, at first, anterior to the fifth gill-cleft. No muscle-plate is developed in the fourth branchial segment.

The differences in the ventral branchial muscles are as follows: (1) In Menopoma there is a Transversus ventralis iv, and no Transversus ventralis iii. In Necturus there is a Transversus ventralis iii, and no Transversus ventralis iv. (2) In Menopoma two Subarcuales, i.e. the second and third, become Subarcuales obliqui ii and iii. In Necturus only one Subarcualis, i.e. that of the second branchial arch, becomes a Subarcualis obliquus ii. (3) In Menopoma Subarcualis rectus iv extends forward to Branchiale i. In Necturus it is Subarcualis rectus iii which extends forwards to Branchiale i.

There is so great a similarity between the muscles of the fourth branchial segment in Menopoma and those of the third branchial segment of Necturus, that it is improbable that the difference is due to transformation of the characteristics of the third branchial arch musculature of Menopoma into those of the third of Necturus, or conversely; nor is there any evidence of the dropping out, or intercalation, of a branchial bar between the first and last.

This suggests that a common branchial muscle-plate has been separated into four portions by the gill-clefts in Menopoma; whilst in Necturus it has been separated into three portions by the gill-clefts.

No one branchial bar of Necturus, with its related muscles, is thus exactly homologous with any one branchial bar of Menopoma, and it is only possible to speak of a collective homology.

Branchial segments may thus be reduced in number by at least two processes, by a separation of the branchial area into a fewer number of segments without loss of any one individual segment, or by a loss of the ultimate segment. The former is apparently what happens in Necturus and Proteus, as compared with Menopoma and Ellipsoglossa. The latter is apparently what happens in Amphibia generally, as compared with Dipnoi. In Dipnoi there is a fifth branchial bar and related muscles. In Menopoma and Ellipsoglossa there is an empty fifth branchial segment. In Rana there is no developmental evidence of a fifth branchial segment. The existence in Necturus of an empty fourth branchial segment suggests that the mutation to three branchial segments took place subsequent to the loss of a fifth branchial bar and related muscles.

After formation of the full number of segments, the branchial region may

become shorter by fusion. Thus Sarasin showed that, in Ichthyophis, the third and fourth branchial bars coalesce. Comparison of the 5·9 cm. larva of Ichthyophis with the, relatively later, 7 cm. larva of Siphonops suggests that this is accompanied by fusion of Levatores iii and iv, and by disappearance of Subarcualis rectus iv.

Development of the larynx and laryngeal muscles

Greil stated that in Urodelan and Anuran larvae the lungs are developed from bilateral longitudinal grooves on the inner surface of the floor of the oesophagus, forming with each other an angle of about 40°, open caudally. These grooves develop at a period when only four gill-clefts are present; the fifth and sixth being formed later, between the fourth and the primordia of the lungs. The pulmonary grooves form pocket-like diverticula, which grow backwards in the thickened splanchnopleure and develop into the primitive pulmonary sacs. The pulmonary grooves are put into communication with each other by a transverse or bifurcation groove. The ventral portion of the wall of the oesophagus, in front of the bifurcation groove, forms by approximation of its walls the longitudinal laryngo-tracheal groove. It is continuous posteriorly with the bifurcation groove. In Anura it becomes temporarily closed by union of its walls, and is subsequently hollowed out into the laryngo-tracheal groove. The pulmonary and bifurcation grooves are folded off on their dorsal and caudal side from the oesophagus.

In Anura the sixth gill-clefts remain rudimentary and have no connection with the ectoderm; in Bombinator they atrophy, in other Anura the ultimo-branchial bodies are formed from their ventral portions. In Ranidae and Bufonidae the lumen of the anterior part of the oesophagus becomes temporarily obliterated and subsequently opens out—later than does the laryngo-tracheal cavity.

In Urodela (Triton, Salamandra, Siredon) the sixth gill-clefts, which are also transitory, reach the ectoderm-bands which grow towards them and fuse for a short distance. Rupture to the exterior does not take place. The ultimo-branchial body is developed from the left sixth cleft.

Greil did not investigate the development of the laryngeal-muscles.

Anura. In a 7 mm. larva of Rana temp. (figs. 3, 4, 5), the laryngeal groove extends from 75μ behind the sixth gill-clefts, where it passes into the transverse pulmonary groove, forwards to 15μ behind the sixth gill-clefts. Like the oesophagus above, it has no lumen. The coelom extends dorsally on either side of the transverse groove to the side of the oesophagus, but does not do so laterally to the laryngeal groove. Many undifferentiated cells are visible on either side of the oesophagus and laryngeal groove, proliferated from the visceral layer of the coelom (figs. 4, 5).

In a $7\frac{1}{2}$ mm. larva the laryngeal groove extends from 67μ behind to the level of the sixth gill-clefts. On either side of the laryngeal groove is seen

the primordium of the laryngeal muscles, partially separated into the Constrictor and Dilatator laryngis (figs. 6, 7). It extends from 82μ behind to 22μ behind the sixth gill-clefts.

In an 8 mm. larva (figs. 8, 9, 10) the laryngeal groove extends from 60μ behind to 7μ in front of the sixth gill-clefts. There is a lumen in its ventral part, continuous with that in the transverse groove. The laryngeal muscles (figs. 9, 10) are fully formed, and extend from 127μ behind to 15μ behind the sixth gill-clefts. The Constrictor meets its fellow dorsally and ventrally.

In an 11 mm. larva (figs. 13–16) the laryngeal groove extends from 22μ behind the sixth gill-clefts to 37μ in front of them. The laryngeal muscles extend from 195μ behind to 22μ in front of the sixth gill-clefts. The primordium of the arytenoid s. pars laryngea cart. lat. is visible within the Constrictor laryngis. The Constrictor oesophagi is visible lateral, and ventral, to the forepart of the oesophagus.

The laryngeal groove is thus at first wholly posterior to the sixth gill-clefts, and gradually extends forwards, so that finally its anterior end is a little in front of them. The lumen in the transverse pulmonary groove extends forwards in the laryngeal groove, which opens by separation of its lips. There is no trachea. The laryngeal muscles are formed in the splanchnic mesoderm on either side of the laryngeal groove, and become fully developed behind the sixth gill-clefts. In their subsequent growth they spread backwards and forwards, so that the ventral part of the obliquely situated Constrictor laryngis comes to lie a little in front of the sixth gill-clefts, i.e. in the fourth branchial segment. There is no migration forwards of the laryngeal muscles.

The Constrictor laryngis posterior is not formed until metamorphosis begins. In a 20 mm. larva (figs. 18 and 19) there are a number of oval cells in the angle, open backwards, of the muscle-fibres of the Constrictor laryngis diverging from the ventral raphé. In a later larva (fig. 20)—one with hind legs just visible on the surface of the body—these cells have grown into muscle-cells, which pass upwards and backwards forming the primordium of the Constrictor laryngis posterior. These phenomena confirm the statement of Wilder that the Constrictor laryngis posterior is a derivative of the Constrictor laryngis.

Gymnophiona. In Ichthyophis five gill-clefts were mentioned by the Sarasins. In Hypogeophis Marcus described seven gill-clefts, of which the first six break through. The sixth totally atrophy. The seventh do not reach the ectoderm and form the ultimo-branchial bodies which separate from the hypoblast and develop into a small vesicle on each side. The primordium of the lungs is first seen in stage 22 in which the fifth gill-clefts are already formed, either as two lateral bulges ventral to the gut, of which the left disappears, or as a right sided one—which (from the figure given) is apparently on the level of the seventh gill-clefts. Marcus did not describe any later stages in the formation of the larynx.

Göppert stated that the laryngeal muscles of a late Ichthyophis larva

consist of a Dilatator laryngis, a Constrictor laryngis, and a Laryngeus ventralis. The first-named takes origin from the fourth branchial bar and is inserted into the lateral process of the Cartilago laryngis; the Constrictor laryngis consists of two half rings surrounding the Cartilago laryngis just behind the attachment of the Dilatator; and the Laryngeus ventralis takes origin from the lateral process of the Cartilago laryngis and passes downwards just in front of the Constrictor and meets its fellow in a ventral median raphé. The existence of a Laryngeus dorsalis was doubtful.

These structures are all present, as described by Göppert, in earlier Ichthyophis larvae, and in a late Siphonops larva. In both, however, the existence of a Laryngeus dorsalis is certain (figs. 25, 29, 30).

In adult Siphonops the Laryngei dorsalis and ventralis have disappeared, and the Constrictor is more developed. In adult forms of Hypogeophis and Caecilia the Dilatator, Laryngei, and Constrictor are all present.

Göppert also described, in a late Ichthyophis larva, a Hyo-pharyngeus internus, taking origin from the fourth branchial cartilage and from the connective tissue lateral to the pharynx and passing round it to a median aponeurosis between the pharynx and trachea and to the lateral side of the trachea.

The muscle is present in younger Ichthyophis larvae and in larval and adult Siphonops. In the 3·5 cm. larva of Ichthyophis the hinder part of the muscle is overlapped by the anterior edge of the Constrictor oesophagi, and in the Siphonops larva it is, though present, less developed—incompletely separated from the Constrictor oesophagi and with no median raphé (fig. 31).

These phenomena suggest that the muscle is a separated portion of the anterior edge of the Constrictor oesophagi which has gained attachments to the fourth branchial cartilage.

Göppert described, as one of the laryngeal muscles in a late Ichthyophis larva, fibres springing from the dorsal fascia and inserted into that covering the anterior part of the ventral trunk-muscles.

It is not yet developed in 3·5 and 5·9 cm. Ichthyophis larvae. In a 7 cm. Siphonops larvae it is a slightly marked muscle lying just lateral to and behind the fused third and fourth branchial cartilages and tendon of Levator iv, with no dorsal or ventral attachment (fig. 31). In the adult Siphonops it forms a well-marked muscle arising from the dorsal fascia just behind Levator iv, and passing downwards outside the fused third and fourth branchial cartilages to a median raphé just behind Transversus ventralis iv. These phenomena suggest that the muscle in question is possibly a derivative of Levator iv. There are, in Ichthyophis larvae and in larval and adult Siphonops, three muscles arising in common from the dorsal fascia some distance behind Levator iv—one passes downwards and inwards above the oesophagus, the second passes downwards laterally to the oesophagus and is inserted into the fascia on the medial surface of the Rectus and also to a median raphé which is connected with the skin between the two Recti, whilst the third passes

downwards and outwards lateral to the Rectus. The muscles do not appear to have any genetic relation either to the Levatores or to the laryngeal muscles.

Urodela. In a 15 mm. larva of Menopoma (figs. 32–35) laryngeal and transverse grooves are present, both continuous with the epithelium of the branchial region and oesophagus. The front edge of the laryngeal groove is 40μ in front of the anterior border of the sixth gill-cleft; it is 180μ long, extending back to the level of the hinder border of the (unseparated) sixth and seventh gill-clefts, where it passes into the transverse groove. In a larva of 17 mm. (figs. 36, 37) the conditions are the same, but, owing to growth, the laryngeal groove is 200μ long. In a larva of 19 mm. (figs. 42–45) the length of the laryngeal groove is 330μ of which the posterior 30μ and the transverse groove have separated from the oesophagus. The anterior end of the laryngeal groove is 40μ in front of the stump of the sixth gill-cleft, and it passes into the transverse groove 90μ behind the border of the seventh gill-cleft. In a larva of 22 mm. the length of the laryngeal groove is 330μ, of which the anterior 160μ is attached to the epithelium. Its front end is 70μ behind the stump of the sixth gill-cleft, and 110μ in front of the seventh gill-cleft. In a larva of 24 mm. (in which the seventh gill-cleft has disappeared) the anterior end of the laryngeal groove is 150μ behind the stump of the sixth gill-cleft; in one of 28 mm. it is 260μ behind.

Two processes thus take place; a separation, from behind forwards, of the transverse and hinder part of the laryngeal groove from the oesophagus, and possibly a subsequent slight backward migration; but in a larva of 22 mm. —the latest in which the seventh gill-cleft is present and demarcation of the branchial region from the oesophagus thus possible—the anterior end of the laryngeal groove is in the fifth branchial segment and the larynx is situated in the hindmost branchial segment and the forepart of the oesophagus.

In larvae of 15 and 18 mm. (figs. 32–35 and figs. 38–41) the epithelium of the pericardium and pericardio-peritoneal ducts, underlying the laryngeal and transverse grooves, is thickened and proliferating cells which spread up round those grooves. In a larva of 19 mm. (fig. 45) these cells have increased in number and spread dorsally round the oesophagus. Those immediately round the laryngeal groove are undifferentiated, whilst the Constrictor oesophagi and Dilatator laryngis are slightly marked out by the cells being long-oval in shape. In a larva of 22 mm. (fig. 47) the Constrictor oesophagi and Dilatator laryngis are quite distinct from the surrounding splanchnic mesenchymatous cells. The Dilatator laryngis has spread upwards, its dorsal end being lateral to the spinal musculature. In a larva of 24 mm. (fig. 50) the Laryngei are visible in front of the lower end of the Dilatator. In one of 28 mm. (fig. 52), the Constrictor laryngis is visible behind it and the primordium of the arytenoid is distinguishable.

In a 12 mm. larva of Necturus the front end of the laryngeal groove is in the third branchial segment, 50μ in front of the fifth gill-cleft; its length is

170μ. In a larva of 13 mm. the front end of the laryngeal groove is in the fourth branchial segment, 30μ behind the stumps of the fifth gill-cleft, its length is 70μ, and it passes into the transverse groove at the posterior edge of the sixth gill-clefts. In a larva of 15 mm. the front end of the laryngeal groove is 100μ behind the stumps of the fifth gill-clefts, and in one of 17 mm. 150μ behind. In subsequent stages the stumps of the fifth gill-clefts have become detached from the endoderm.

In larvae of 12 and 13 mm. (figs. 57–59, and 60–62) the splanchnic layer of the coelomic epithelium round the laryngeal and transverse grooves is thickened and proliferating cells which spread round these grooves and the oesophagus. In a larva of 15 mm. (fig. 63) the primordia of the Constrictor oesophagi and Dilatator laryngis are visible in this splanchnic mesoderm. In a larva of 17 mm. (fig. 69) the Dilatator is more marked and its upper end has spread up laterally to the spinal musculature. The Laryngei are formed; their lateral ends are continuous with the Dilatator laryngis and do not arise from the primordium of the arytenoid. In a larva of 20 mm., the trachea has developed, 80μ in length, and the Dilatator tracheae has separated from the Dilatator laryngis. In a larva of 42 mm., as shown by Göppert, the Laryngei arise from the arytenoid.

Morphology of the larynx and laryngeal structures in Amphibia

On reviewing the above observations it is clear that, in the Amphibia examined, the transverse groove lies behind the ultimate gill-cleft, in the oesophageal region. The laryngeal groove extends forward into the ultimate (Rana) or penultimate (Menopoma, Ellipsoglossa, Necturus) branchial segment. In the latter three animals, the front end of the laryngeal groove subsequently migrates slightly backwards into the ultimate segment. The transverse groove and hinder part of the laryngeal groove are constricted off from the oesophagus. The larynx thus comes to lie in the ultimate branchial segment and the forepart of the oesophagus. The front end of the larynx subsequently lies at steadily increasing distances behind the remains of the penultimate gill-cleft or -clefts, but as this occurs after loss of the ultimate gill-clefts its meaning is doubtful. It may be simply a growth phenomena and not indicate any real backward migration. The oesophageal and laryngeal muscles and the laryngeal cartilages are differentiated from cells which are proliferated from the splanchnic layer of the coelomic epithelium—pericardium and pericardio-peritoneal ducts. The cells spread round the oesophagus and larynx. The oesophageal and laryngeal muscles become differentiated among these cells. Although, phylogenetically, the laryngeal muscles may be regarded as derivatives of the Constrictor oesophagi, in actual development they are not budded or split off from it, but the two sets of muscles develop concurrently in close proximity in the splanchnopleure sheath of the oesophagi.

Comparison of the various laryngeal muscles leads to the following conclusions. *Dilatator laryngis.* In Anuran larvae the Dilatator arises from the

connective tissue ventro-lateral to the oesophagus and passes inward and forwards to the arytenoid. In the adult, the origin of the muscle becomes attached to the processus postero-medialis. In Gymnophiona (larva and adult), the muscle arises from the ventral part of the fourth branchial cartilage, and is inserted into the arytenoid. In Urodela the origin of the muscle extends upwards round the spinal musculature to the dorsal fascia (hence the name "Dorso-laryngeus" often applied to it).

Göppert, who (*vide* p. 133) was of opinion that the Dilatator is serially homologous with Levatores arcuum branchialium, thought that its form in Urodela is primary and that the conditions in Anuran larvae and in Gymnophiona are secondary.

But, as shown above, the Subarcuales of the branchial bars are more primitive in Anuran and Gymnophionan larvae than in Urodela, and the Dilatator is developed by upward extension from a primordium ventro-lateral to the forepart of the oesophagus. It follows that there is no *a priori* probability that the form of the Dilatator in Urodela is primitive and the phenomena of its development are against such a view. It is possible then that its form in Anuran larvae is the primitive one, and that those in Urodela and Gymnophiona represent two divergent secondary conditions.

Constrictor laryngis and Laryngei. In Anuran larvae a Constrictor laryngis is developed, encircling the arytenoid posterior to the insertion of the Dilatator. In Gymnophionan larvae Laryngei and a Constrictor are present, the former in front and the latter behind the insertion of the Dilatator. In Urodelan larvae, other than Necturus, Proteus, and Siren, Laryngei and a Constrictor are present, the former in front and the latter behind the insertion of the Dilatator. In Necturus, Proteus, and Siren, Laryngei only are present—a Constrictor is not developed.

Drüner stated that in Salamandra and Triton the Laryngei disappear at metamorphosis. The same is also true of Siphonops.

Göppert held that the Constrictor is proliferated from the Laryngei ventrales in Siredon, where there is a slight overlap of these muscles. But in Menopoma there is no overlap and, though the Laryngei are developed at an earlier stage, yet there is no indication that the Constrictor is developed from them.

It would appear then that the Laryngei and Constrictor are independent laryngeal constrictor muscles, of somewhat different form, developed in front of and behind the insertion of the Dilatator.

It is not known whether the absence of Laryngei in Anura is a primitive or a secondary feature. On comparison with Dipnoi (see later), it would appear that probably a Constrictor is, phylogenetically, the older structure.

The absence of a Constrictor in the Perennibranchiata, Necturus, Proteus, and Siren, is probably to be explained by the occurrence of its development at a somewhat later stage than the Laryngei, taken in association with the theory of Boas that the Perennibranchiata are persistent larval forms—

Urodela which no longer have a metamorphosis. Menopoma would be similar if development ceased at the stage of 24 mm.

Göppert (*vide* p. 132) held that the form of the arytenoids, and the attachment of the Laryngei to them, in Necturus and Proteus represents the primitive condition. But the developmental phenomena appear to negative such a view and to show that, as Drüner thought, the condition is secondary to a more primitive one, in which, as e.g. Triton, the arytenoids are narrower and the Laryngei take origin from the Dilatator.

In Siren (*vide* Drüner) there are, in front of the Dilatator, Laryngei, arising partly from the arytenoid and partly from the Dilatator, but no Constrictor. There are, however, outside the Laryngei, sphincter fibres, which have no homologues in other Amphibia. The condition needs embryological investigation—possibly the sphincter fibres are proliferated or separate from the Laryngei.

From the slightly different innervation of the Dilatator laryngis and of the Constrictor laryngis and Laryngei Drüner inferred (*vide supra*, p. 134) that these muscles have been derived from different segments. This is not borne out by developmental phenomena. Further, in Anura and Gymnophiona all the laryngeal muscles are innervated by the N. recurrens. The phenomena in Urodela are simply due to a slightly earlier giving off of the branch for the Dilatator from the N. intestino-accessorius, and have no morphological importance.

Cartilago lateralis. Anura. Märtens (1895) stated that in Rana temp. there is no continuous cartilago lateralis which afterwards separates into cartilago arytenoidea and C. laryngo-trachealis, but that these elements are separate from the first, the arytenoid developing during metamorphosis, and the four elements which fuse to form the annulus shortly afterwards.

I find that the arytenoid is present in a 12 mm. larva, in a precartilaginous condition, quite distinct from the surrounding mesoblast. There is no trachea at this stage, and during the rest of larval life the larynx immediately bifurcates into the two bronchi (fig. 17). In a larva during metamorphosis, at the stage when the tail has shrunk to half its original length, the trachea develops and the elements of the annulus appear. They are continuous with the dorsal end of the obliquely placed arytenoid by precartilaginous tissue (figs. 21 and 22).

Gymnophiona. In a 3·5 cm. larva of Ichthyophis the trachea is already formed. There is a precartilaginous arytenoid, which anteriorly is circular in shape, then broadens (with attachment of the Dilatator laryngis to its outer edge, and the Laryngei above and below) and then contracts. It is continuous posteriorly with a cellular sheath, thicker dorsally than ventrally, round the trachea. In a 5·9 cm. larva the arytenoid has chondrified and is continuous with a cellular sheath round the trachea. In this sheath are incomplete ring-shaped patches of cartilage.

In a 7 cm. larva of Siphonops the conditions are similar to those of the

5·9 cm. Ichthyophis larva (fig. 31). In the adult, with the disappearance of the Laryngei, the lateral projection of the arytenoid also disappears and its hind end is continuous with the first tracheal ring.

Urodela. A precartilaginous arytenoid is present in a 10 mm. larva of Triton cristatus. It is chondrified in a larva of 12 mm. No trachea is present in larvae up to a length of 28 mm. and correspondingly there is no pars laryngea. A trachea, 135μ in length, has developed in a larva of 33 mm. (figs. 77 and 78). Behind the arytenoid, and continuous with it, is a cellular mass lateral to the trachea. This cellular mass is chondrified as the trachea bifurcates into the bronchi. Later on, as described by Drüner, there are many cartilaginous islands along the trachea, and subsequently, as described by Gegenbaur, a continuous arytenoid and tracheal skeleton—the cartilago lateralis.

Similarly, in Salamandra, the first cartilage developed in the tracheal sheath is found at its bifurcation into the bronchi, in a 25 mm. larva.

In a 28 mm. larva of Menopoma there is no trachea, the larynx immediately bifurcating into the bronchi. A precartilaginous arytenoid is present, with flat internal and convex external surface, and its posterior end ventral to its anterior end (fig. 52). In a larva of 32 mm. a trachea, 120μ in length, has developed. This is not accompanied by any forward migration of the larynx relative to the branchial skeleton; by it the bifurcation of the respiratory tract is carried further back. The arytenoid is chondrified and has a slight lateral process at the insertion of the Dilatator laryngis. The arytenoid is continuous with a cellular sheath lateral to the trachea (fig. 55). In a larva of 34 mm. the primordium of the processus trachealis has developed in the cellular tracheal sheath, dorsal to the posterior end of the arytenoid (fig. 56). In a 40 mm. larva this process is continuous with the arytenoid. In the adult (Drüner) many cartilaginous islands have developed in the tracheal sheath.

In a 17 mm. larva of Necturus (Fig. 69) the arytenoid is present as a precartilaginous mass of cells extending laterally to the larynx, but not sufficiently far for the Laryngei to arise from it. They are continuous laterally with the Dilatator laryngis. In a 42 mm. larva, as shown by Göppert, the arytenoid is broader and the Laryngei arise from it. There is no trachea in larva up to a length of 18 mm. In one of 20 mm. (fig. 70) a trachea, 80μ long, has developed. Lateral to the trachea is a sheath of connective tissue, which is continuous anteriorly with the arytenoid.

It follows from the above that the simplest and probably the most primitive form of the arytenoid is a roundish rod, surrounded by the Constrictor laryngis and with a Dilatator laryngis attached to its anterior end. This is present in Anuran larvae. In Gymnophionan and Urodelan larvae the arytenoid is relatively longer, in relation to the presence of the Laryngei. The condition, in Necturus and Gymnophionan larvae, of a broad plate with Laryngei arising from it, is probably secondary to a simpler condition such as is present in Triton. In this connection it is of interest to see that in Siphonops the arytenoid becomes roundish in outline on the atrophy of the Laryngei.

The development of the pars trachealis cartilaginis lateralis is related to the formation of a trachea which develops at the end of the larval stage in Rana, during larval life in Menopoma, Amblystoma, Triton, Siphonops and Ichthyophis, and in the 20 mm. stage of Necturus. The pars trachealis is formed as a non-chondrified backward prolongation of the pars laryngea s. arytenoid. It may persist in this condition, e.g. Necturus, or may subsequently chondrify in tracts of more or less complete rings. In Triton and Salamandra the cartilage is first developed at the bifurcation of the trachea.

The above discussion shows that further embryological investigations are needed—in particular it would be well to know the condition of the branchial skeleton and ventral branchial muscles in the larvae of Amphiuma[1] and Cryptobranchus jap., the development of the sphincter laryngeal fibres in Siren, and the development of the ventral branchial muscles, larynx and laryngeal muscles in Gymnophiona.

On the phylogenetic history of the larynx, trachea, and laryngeal muscles

Schmidt (1913), who investigated the development of the larynx in certain Reptiles, was of opinion that the lungs of Polypterus, Amphibia, and Amniota, like the swimming bladder of Lepidosteus and Amia, develop in the same native soil ("Mutterboden"), and that, on the other hand, the trachea with the larynx of Amniota, and possibly also that of Amphibia, are phylogenetically a later formation, the development of which begins with pulmonary respiration.

The larynx of Dipnoi and Polypterus lies in the ventral wall of the gut behind the branchial region. Its musculature was described by Wiedersheim (1904) and Göppert (1904). They came to the conclusion, though without any embryological evidence, that it is developed from pharyngeal musculature and that it represents musculature of atrophied branchial arches.

Neumeyer (1904) and Kellicott (1905), independently, showed that the larynx of Ceratodus is developed in the ventral wall of the gut at some distance behind the branchial region. Greil (1913) confirmed their observations, and also showed that the free mesoderm cells round the gut and larynx become spindle-shaped and develop into smooth muscle cells, which form a mantle round the gut and larynx.

Kerr (1910) stated that in Lepidosiren and Protopterus the lung-rudiment is developed, in stage 32, as a mid-ventral bulging from the pharynx at the level of cleft vi. His figures show that its connection with the gut migrates backwards, so that in stage 35 it is distinctly posterior to the level of the 6th gill-clefts, i.e. is in the oesophageal region. In Lepidosiren, Agar (1907) stated that the ventral and lateral parts of the "Constrictor pharyngis" of Wiedersheim are formed from mesenchymatous cells, budded off from the inner walls of the pericardio-peritoneal ducts, and are thus of splanchnic origin. The dorsal part of the muscle is of somatic origin, being derived

[1] In larvae younger than the 45 mm. stage investigated by Hay.

from myotome Y. He did not investigate the development of the laryngeal muscles, but comparison of his figures with those of Wiedersheim suggests that they are differentiated from the ventral, splanchnic, part of the "Constrictor pharyngis."

Wiedersheim employed the term "pharynx" to denote the portion of the alimentary canal corresponding to atrophied branchial arches. In Lepidosiren, however, there is no embryological evidence that the territory surrounded by the pharyngeal constrictor represents a region of atrophied branchial arches—so that the name is hardly justified. The term "pharyngeal constrictor" in Dipnoi might perhaps be replaced by that of "oesophageal constrictor," though with the reservation that in Lepidosiren and probably Protopterus there is an added constituent from a myotome to its dorsal portion, which is absent in Ceratodus and Amphibia. In this and previous papers the name "pharyngeal" is used as synonymous with "branchial." In this latter sense it may be said that there is no pharyngeal constrictor except in Mammals.

The larynx in Dipnoi is thus developed either in the oesophageal region, or in that of the posterior branchial clefts, and migrates backwards. This variation is similar to that which obtains in Amphibia. On comparison of the figures given by Kellicott in Ceratodus with those of Kerr in Protopterus, it is seen that whereas in Ceratodus the larynx immediately bifurcates, in Protopterus there is a portion of the respiratory tract anterior to its bifurcation. In Amphibia it is the laryngeal groove which, in part, may be situated in the branchial region; the bifurcation groove is posterior to it. If this is so, then the primitive larynx, or what corresponds to it, i.e. the bifurcation groove, is situated in the oesophageal region both in Dipnoi and Amphibia, whilst the laryngeal groove—a later development—is formed in front, and in part in the branchial region.

Wiedersheim held that Protopterus and Lepidosiren, in contrast to Ceratodus, have developed in the direction of Amphibia. The Dilatator laryngis of these two Dipnoi, however, lies on the inner side of the Constrictor laryngis and is not homologous with the Dilatator laryngis s. Dorso-laryngeus of Amphibia which lies on the outside.

On comparison with Dipnoi, the new features in the larynx of Amphibia are (1) Formation of a laryngeal groove in front of the transverse groove, extending forward into the hinder portion of the branchial region. It is possible, however, as suggested above, that there is a laryngeal groove in Lepidosiren and Protopterus. (2) Formation of a Dilatator laryngis on the outside of the Constrictor oesophagi. (3) Formation of Laryngei in Urodela and Gymnophiona. (4) Formation of an arytenoidea. (5) A, late, formation of a trachea, with extension of the arytenoid along it. It is thus possible that the features which are common to Dipnoi and Amphibia are (1) Formation of a transverse groove, or its homologue the larynx in Dipnoi, in the floor of the oesophagus. (2) Derivation of the laryngeal musculature from a pri-

mordium common to it and the Constrictor oesophagi. The only muscle which possibly may be common to Dipnoi and Amphibia is a Constrictor laryngis, which is present in Lepidosiren and Protopterus[1].

In Amniota, as in Amphibia, the transverse groove is developed behind the branchial region in the floor of the oesophagus, and the laryngeal groove is formed progressively forward into the branchial region. The differences from Amphibia are that the laryngeal groove extends into a more anterior branchial segment and that the separation of the respiratory epithelium extends relatively further forward so that the larynx lies entirely in the branchial region. Correspondingly, the primordium of the laryngeal muscles separates from that of the Constrictor oesophagi, migrates forward into the branchial region and there develops into the laryngeal muscles. This method is secondary and related to the secondary position of the larynx.

In Sauropsida the muscles consist of a Dilatator and a Constrictor laryngis which are homologous with those of Amphibia. In a few Reptiles Laryngei are developed. These, like the Constrictor, lie posterior to the insertion of the Dilatator, are modifications of the Constrictor and not homologous with the Laryngei of Urodela and Gymnophiona.

In Mammals the laryngeal muscles consist of a Dilatator, Interarytenoid and Laryngeus ventralis. The Dilatator is homologous with that of Amphibia and Sauropsida and, as in the latter, arises from the Cricoid cartilage. The Interarytenoid represents the dorsal half of a Constrictor. Both the Interarytenoid and Laryngeus ventralis lie in front of the insertion of the Dilatator. Apparently, therefore, they are homologous, not with the Constrictor of Sauropsida and Amphibia, but with the Laryngei of Urodela and Gymnophiona.

Recurrent laryngeal nerve. As the laryngeal muscles are not branchial in origin, their motor nerve—the recurrent laryngeal—is not a branchial nerve. It may be regarded as a specialised oesophageal branch of the vagus. In Gymnophiona and Urodela, and markedly in the latter, it extends to the ventral branchial muscles, supplementing or supplanting branchial nerves.

The phylogenetic history of the recurrent laryngeal nerve is obscure. No nerve was described by v. Wijhe or Beauregard in Ceratodus, nor by Hyrtl in Lepidosiren. Pinkus described, in Protopterus, a fine twig extending from the N. intestinalis to the mucous membrane of the pharynx and larynx, and a R. muscularis and recurrens—a strong branch from the vagus ganglion which passes down on the outside of the "Constrictor pharyngis" and divides into two branches, one of which passes forwards and sinks into the tongue muscles, whilst the other innervates the "Constrictor pharyngis." This last branch was also described by Agar. Neither observer states whether twigs from this R. muscularis to the Constrictor oesophagi can be traced into the

[1] It is to be noted that Greil's investigations of the larynx of Ceratodus did not extend beyond the 18 mm. stage and that Wiedersheim said that the state of his material left much to be desired. So it is possible that Ceratodus, too, has a Constrictor laryngis.

laryngeal muscles. But, whether this be so or not, it is probable that the N. laryngeus recurrens of Amphibia, Sauropsida, and Mammalia may be regarded as being derived from a homologue of this nerve.

Laryngeal and tracheal cartilages. The arytenoid s. pars laryngea cartilaginis lateralis of Amphibia is developed within the Constrictor laryngis or within this and the Laryngei, and like them is differentiated from cells proliferated from the splanchnic layer of the coelomic epithelium. It does not, therefore, represent a fifth, or a more posterior, branchial bar. Its development is probably, as Wiedersheim suggested, dependent on muscle action. It is possibly related to the new development of a Dilatator laryngis in Amphibia. The tracheal skeleton s. pars trachealis cartilaginis lateralis is a backward prolongation of the arytenoid and related to the development of a trachea.

In Sauropsida the ventro-median surface of the Constrictor laryngis may become attached to the hyo-branchial skeleton, but this does not enter into the formation of the larynx.

In Mammalia a thyroid cartilage is formed, derived from two (separate in Monotremes, fused in Marsupials) branchial bars, or from one branchial bar (Eutheria), and the Crico-thyroid muscle is additionally formed from the Constrictor pharyngis, with an innervation from the superior laryngeal nerve. In Monotremes, however, there is a Thyreo-cricoid muscle, innervated by the recurrent laryngeal nerve.

I have, in conclusion, the pleasure of thanking Prof. Watasé for larvae of Ellipsoglossa, J. Pearson, Esq., for larvae of Ichthyophis, Dr Harmer for specimens of Caecilia and Hypogeophis from the British Museum, Prof. J. P. Hill for the loan of sections of an adult Siphonops, and the Bristol University Colston Society for defraying the expenses incurred.

LIST OF FIGURES

PLATES I—XV

The figures are from transverse sections, unless otherwise stated. The lowest number, from any series, denotes the most anterior section.

Rana temp. Figs. 1–22.

Figs. 1–5. Larva 7 mm. long. 1 through 1st and 2nd branchial muscle-plates.
2 „ 2nd and 3rd „ „
3 „ 4th „ „
4 „ the laryngeal groove.
5 „ the transverse groove.

Figs. 6 and 7. Larva 7½ mm. long. 6 through laryngeal groove.
7 „ transverse „

Figs. 8–10. Larva 8 mm. long. 8 through 6th gill-cleft.
9 and 10 through the laryngeal groove.

Figs. 11–16. Larva 11 mm. long. 11 through hypobranchial plate.
12 „ the third branchial bar.
13 and 14 through the laryngeal groove.
15 through the transverse groove.
16 „ the oesophagus and larynx.

Fig. 17. Larva 12 mm. long, through larynx and bronchus; the section is slightly oblique, so that it cuts both larynx and one bronchus.

Figs. 18 and 19. Larva 20 mm. long, through larynx.
Fig. 20. Larva with the hind legs just visible, through larynx.
Figs. 21 and 22. Larva with tail shrunk to half its original length, through trachea.

Ichthyophis glutinosa. Larva 5·9 cm. long. Figs. 23–25. 23 through basihyale, 24 through Transversus ventralis i, 25 through larynx.

Siphonops braziliensis. Larva 7 cm. Figs. 26–31. 26 and 27 through Transversus ventralis i. 28 through Subarcuales recti ii and iii. 29 and 30 through larynx. 31 through trachea.

Menopoma s. Cryptobranchus alleghenienis. Figs. 32–56.

Figs. 32–35. Larva 15 mm. long. 32 through 3rd branchial segment.
33 ,, 4th ,,
34 ,, 6th gill-cleft.
35 ,, transverse groove.

Figs. 36 and 37. Larva 17 mm. long. 36 through 4th branchial segment.
37 ,, 7th gill-cleft.

Figs. 38–41. Larva 18 mm. long, sagittal sections. 38 is the most external.

Figs. 42–45. Larva 19 mm. long. 42 through Subarcuales obliqui ii and iii.
43 ,, Transversus ventralis iv.
44 ,, 7th gill-cleft.
45 ,, larynx.

Figs. 46 and 47. Larva 22 mm. long. 46 through Urobranchiale, 47 through Dilatator laryngis.

Figs. 48–50. Larva 24 mm. long. 48 and 49 through Transversus ventralis iv.
50 through Laryngei.

Fig. 51. Larva 24 mm. long, sagittal section.
Fig. 52. Larva 28 mm. long, through larynx.

Figs. 53–55. Larva 32 mm. long. 53 through Urobranchiale.
54 just behind Urobranchiale.
55 through trachea.

Fig. 56. Larva 34 mm. long, through hinder part of larynx.

Necturus maculatus s. Menobranchus. Figs. 57–70.

Figs. 57–59. Larva 12 mm. long. 57 through 3rd branchial segment.
58 ,, laryngeal groove.
59 ,, transverse groove.

Figs. 60–62. Larva 13 mm. long. 60 through stumps of 5th gill-cleft.
61 ,, 4th branchial segment.
62 ,, laryngeal groove.

Fig. 63. Larva 15 mm. long, through laryngeal groove.
Figs. 64–68. Larva 16 mm. long. 64–66 through 1st branchial bars and Urobranchiale, 67 and 68 through Transversus ventralis iii.
Fig. 69. Larva 17 mm. long, through Dilatator laryngis and Laryngei.
Fig. 70. Larva 20 mm. long, through Dilatator laryngis and Dilatator tracheae.

Ellipsoglossa s. Hynobius nebulosus. Figs. 71–76.

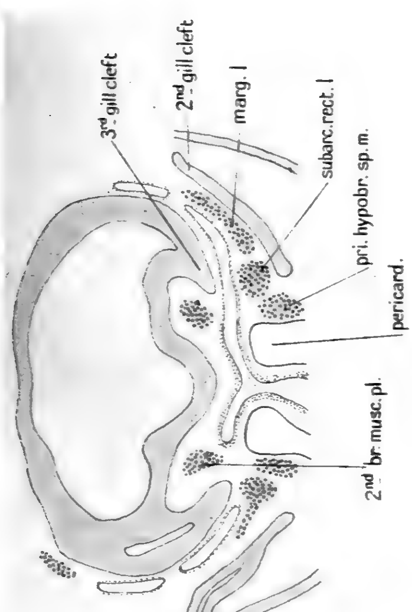
Figs. 71 and 72. Larva 12 mm. long, through 1st branchial bars and Urobranchiale.
Figs. 73–76. Larva 15 mm. long, through Urobranchiale.

Triton cristatus. Figs. 77 and 78.

Larva 33 mm. long, through trachea and bronchi.

ABBREVIATIONS IN FIGURES

Roman numerals	...	cranial nerves
Branch iii and iv	...	fused branchialia iii and iv (in Gymnophiona)
br. musc. pl. ...	...	branchial muscle plate
br. i-hyale ...	...	muscle passing from Ceratobranchiale i to hyale, in Rana
br. ii-hyale ...	...	,, ,, Ceratobranchiale ii to hyale, in Rana
br. aor. arch. ...	...	branchial aortic arch
cerato br. iv ...	...	cerato branchiale iv
cer. hy. ext. ...	...	M. cerato-hyoideus externus
const. oesoph. ...	...	M. constrictor oesophagi



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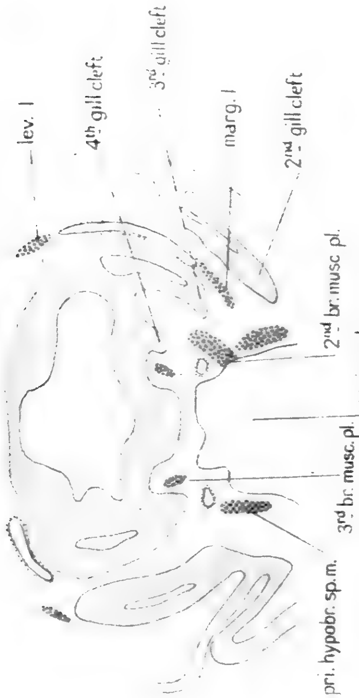

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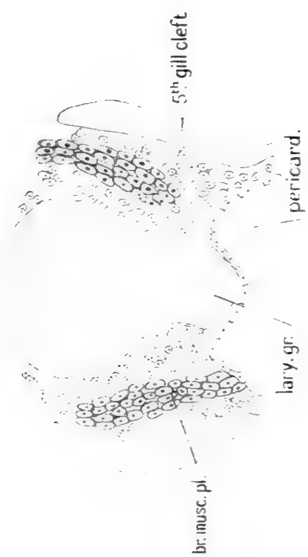

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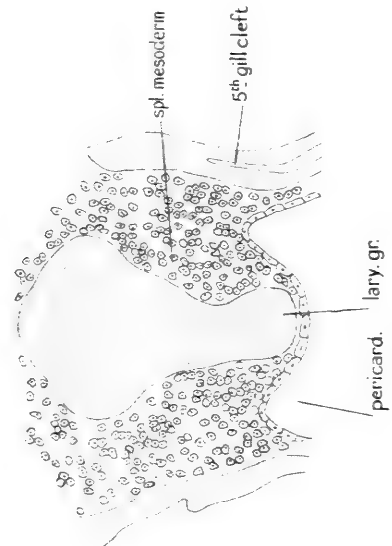
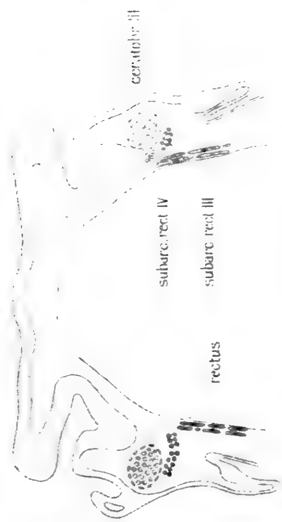


Fig. 4.

Fig. 10.



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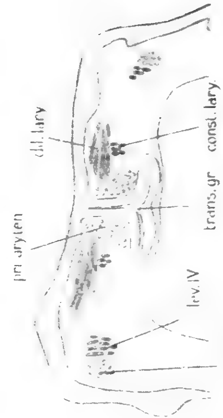

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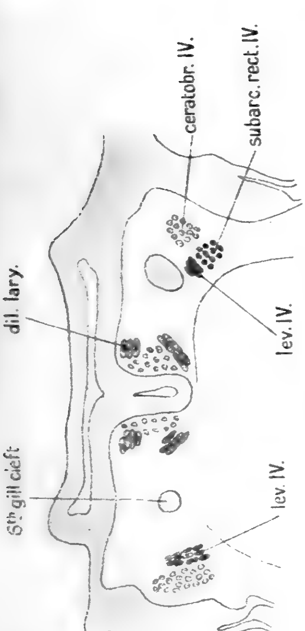

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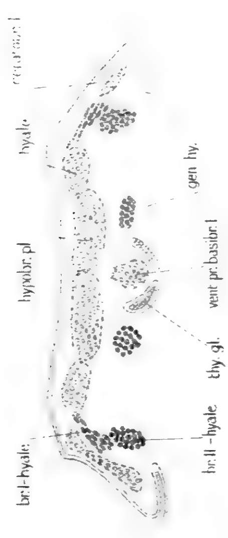

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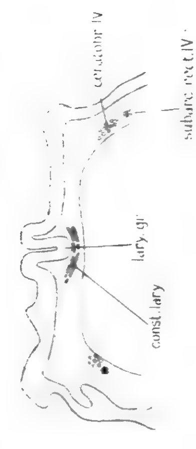
Fig. 14.



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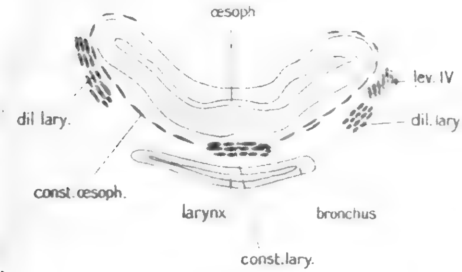

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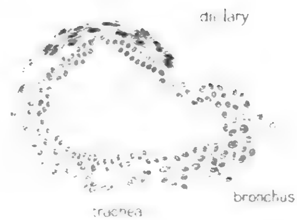

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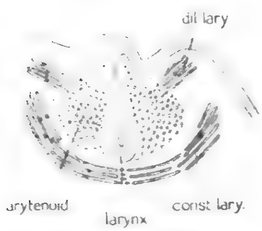

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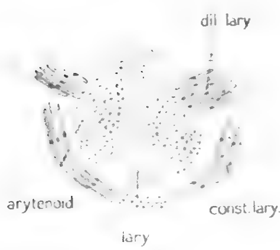

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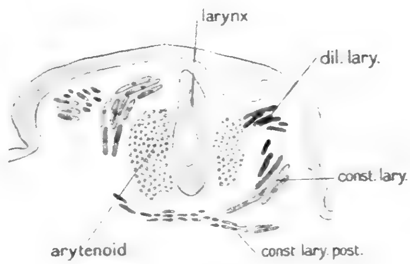

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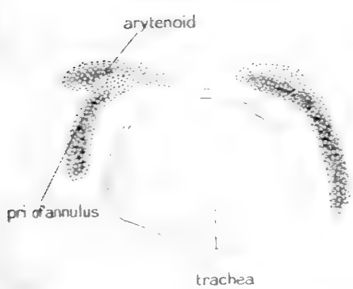

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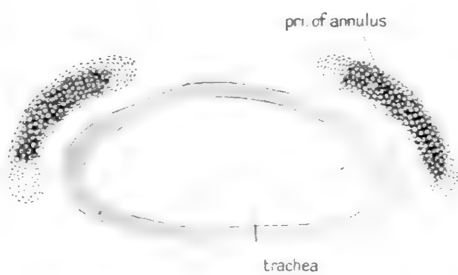

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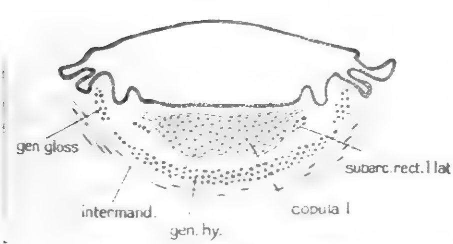

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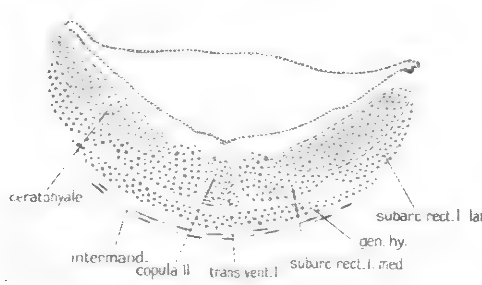

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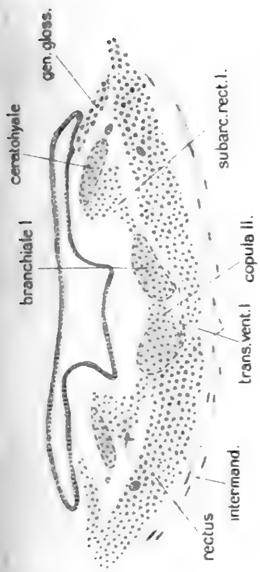

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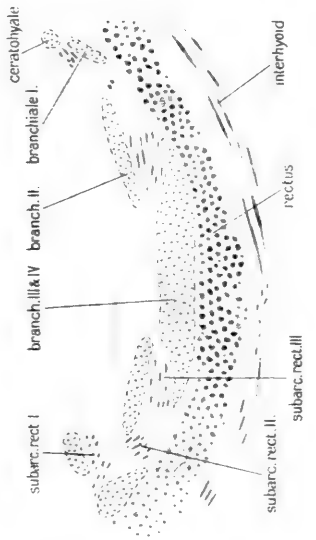

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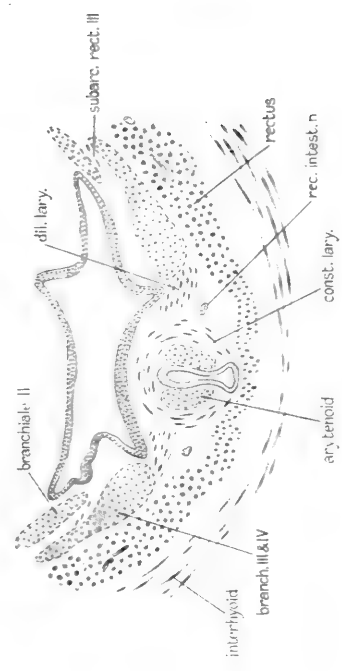

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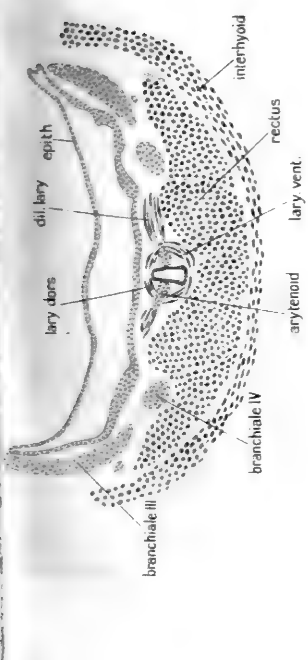

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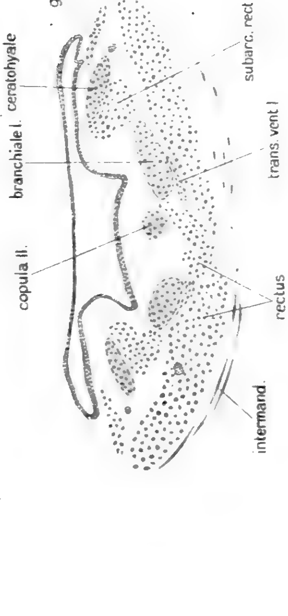

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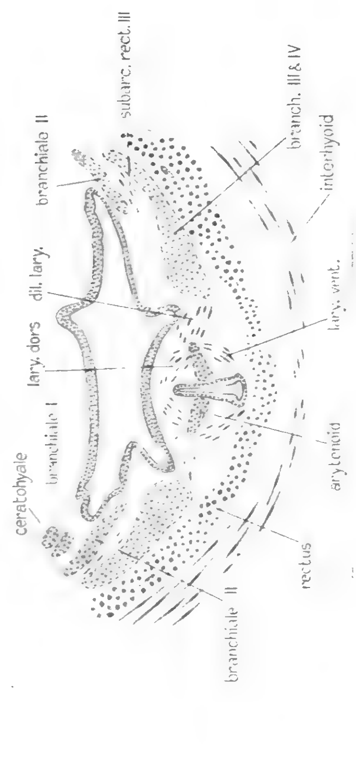

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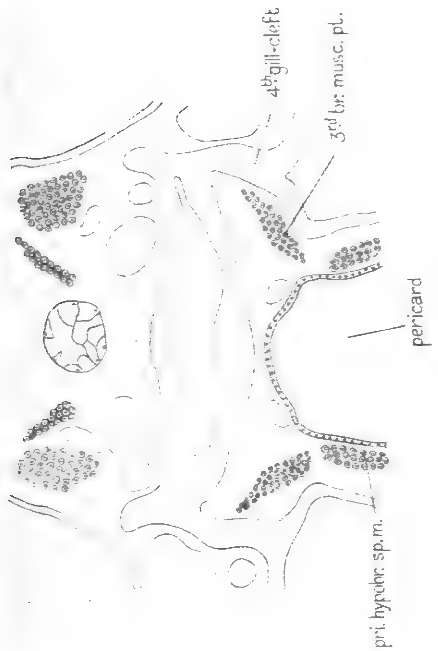

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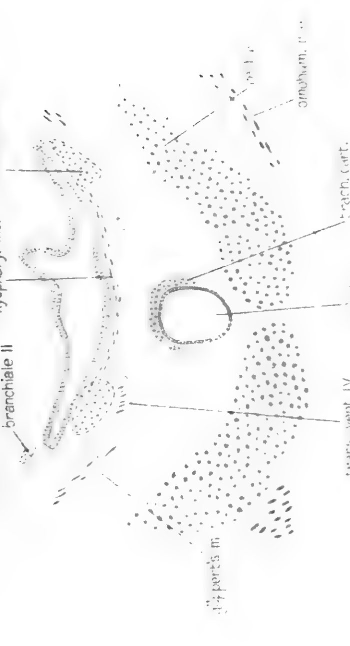

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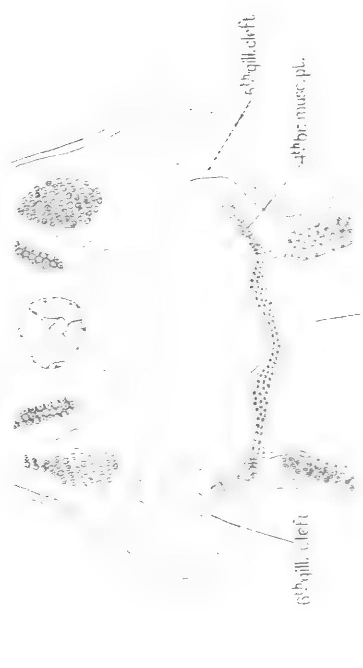

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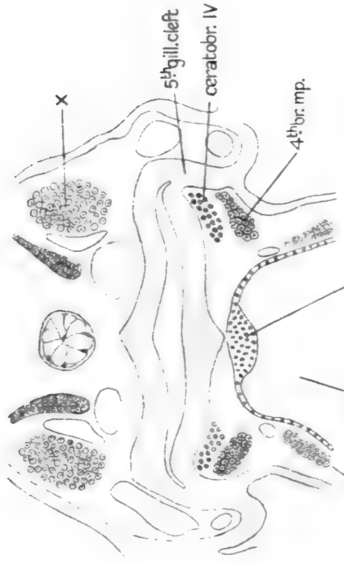

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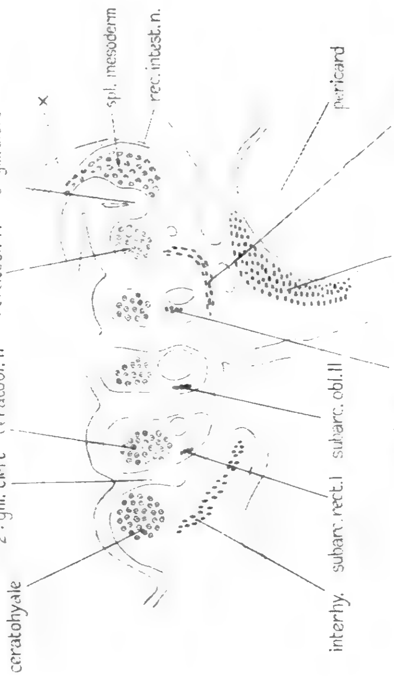

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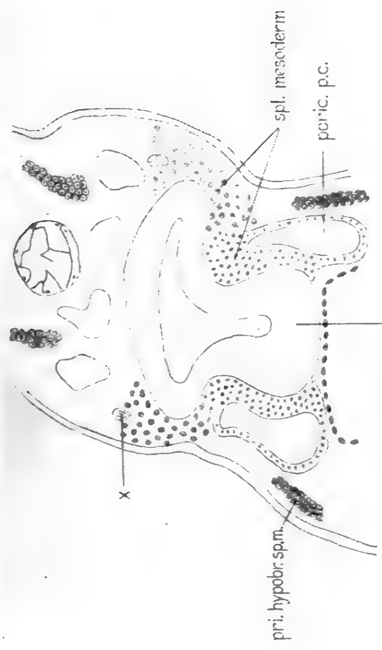

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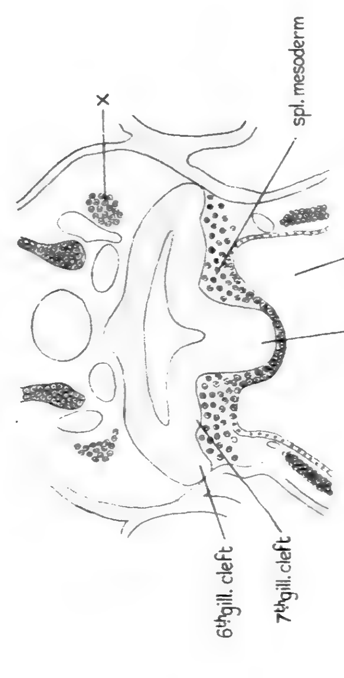

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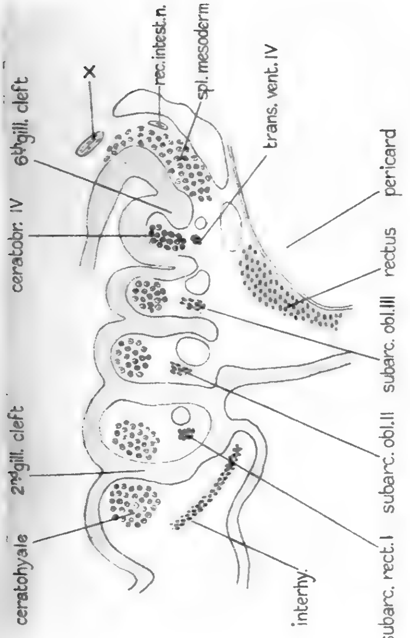

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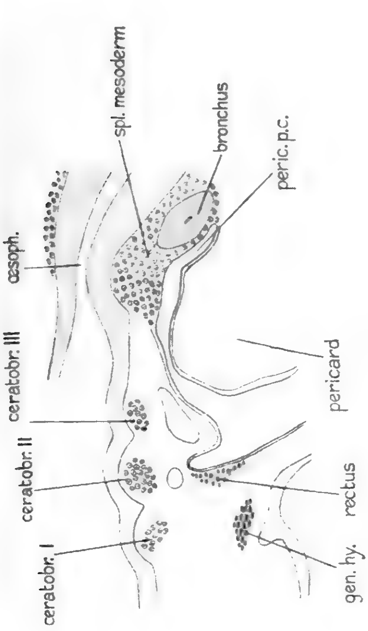

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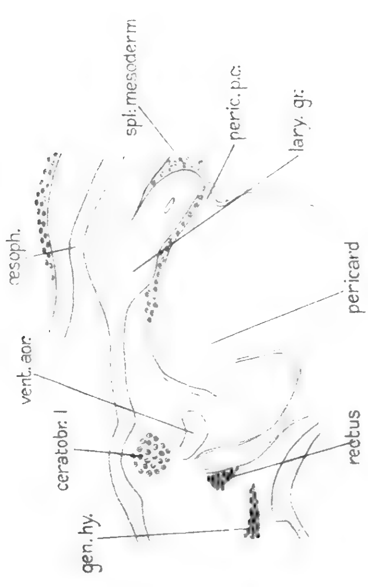

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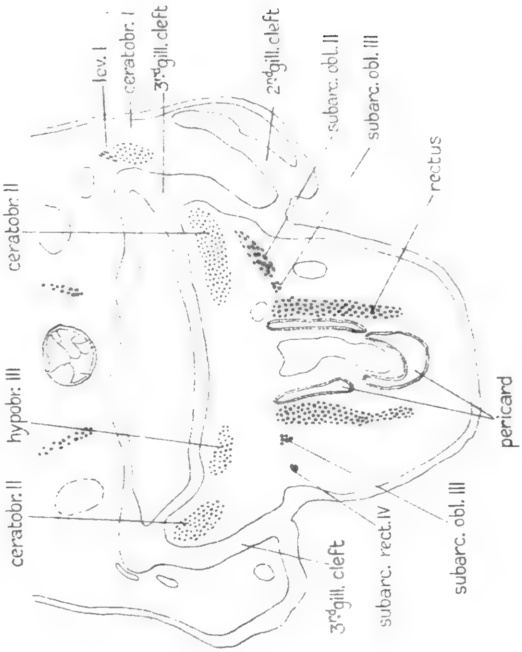

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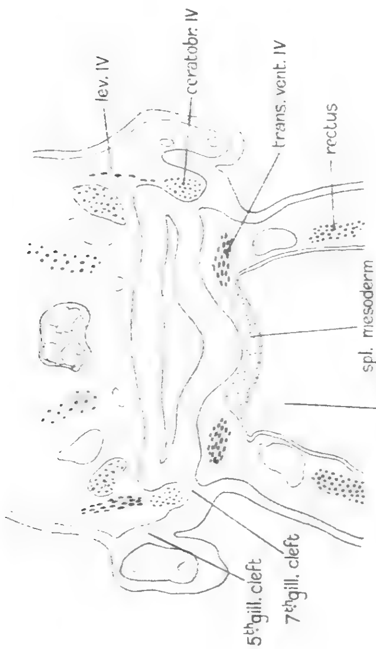

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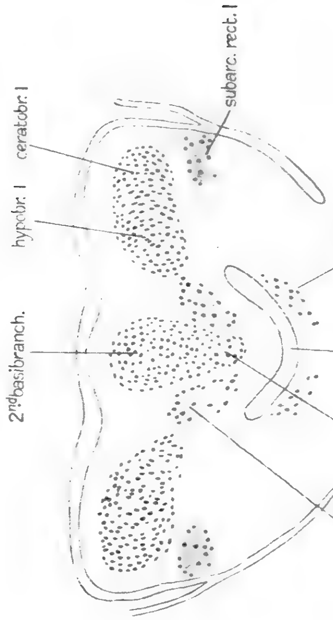

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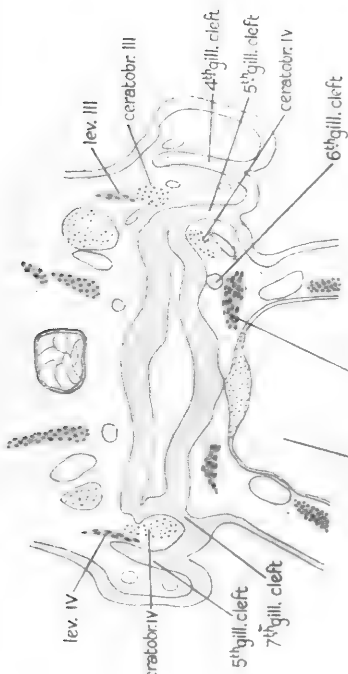

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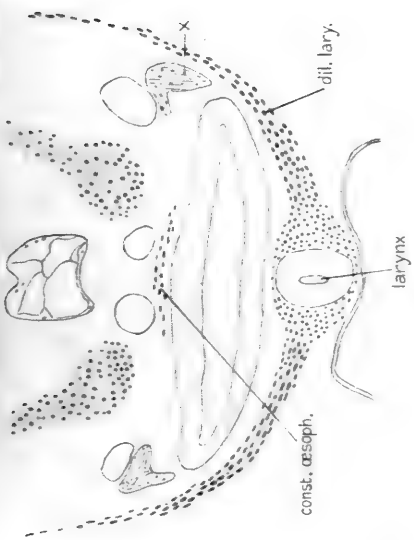

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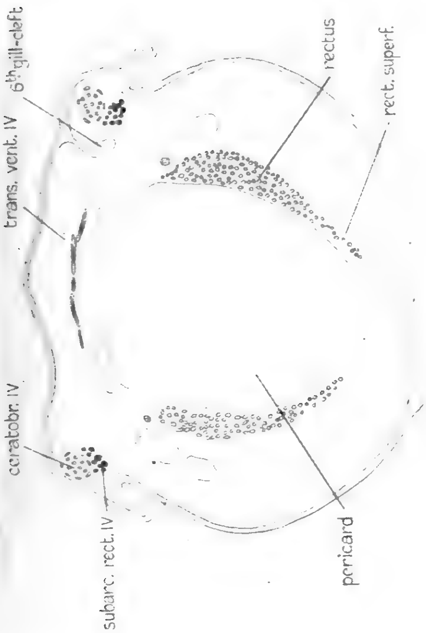

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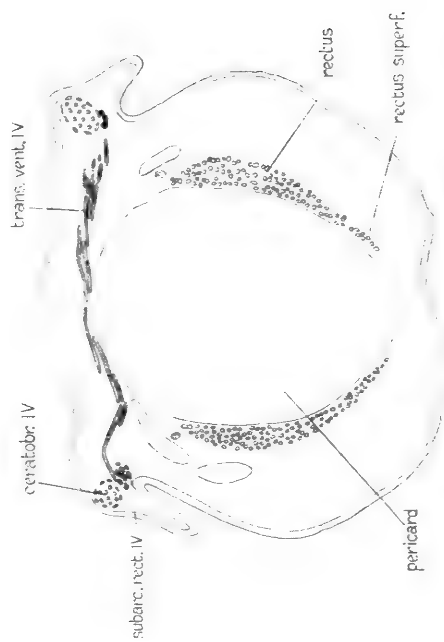

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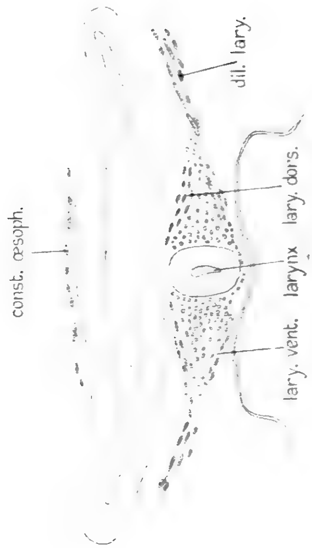

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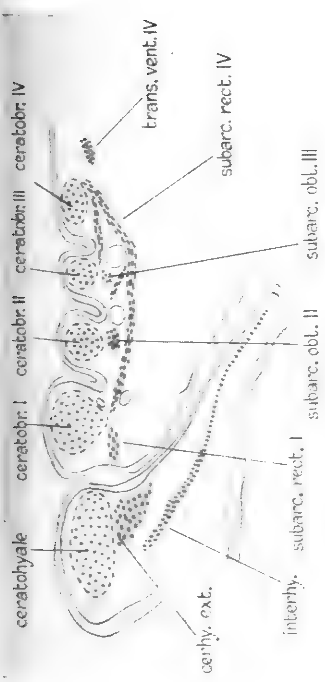

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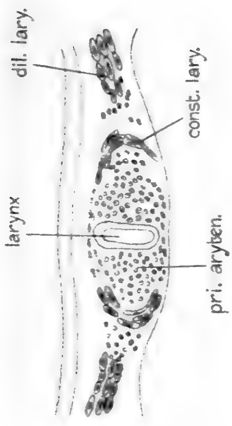

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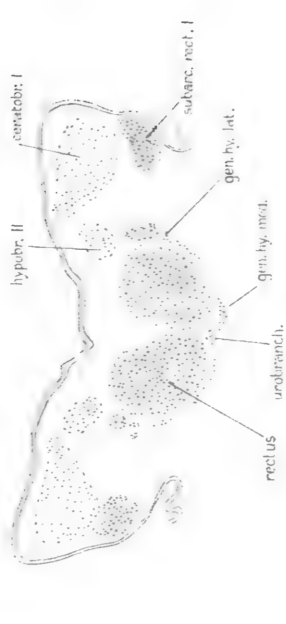

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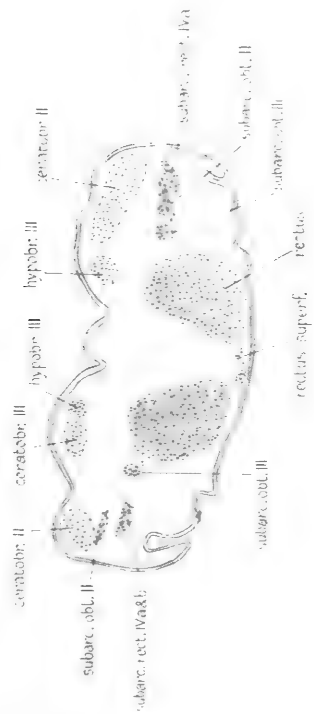

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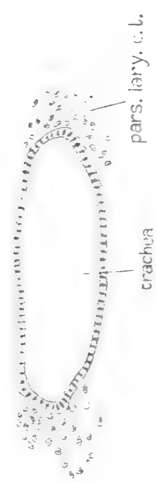

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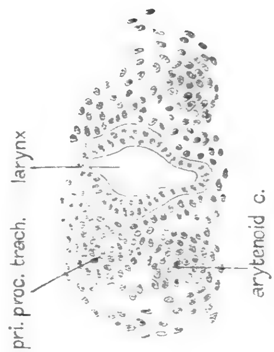

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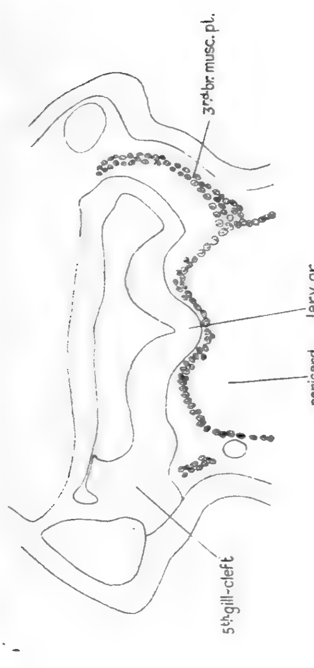

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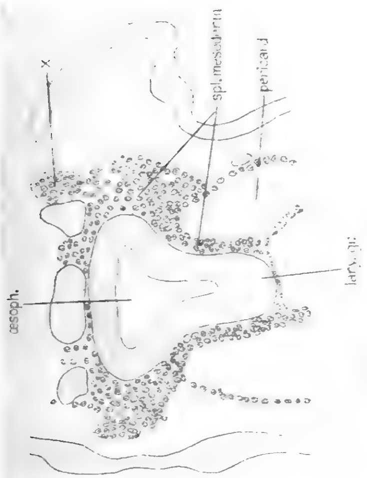

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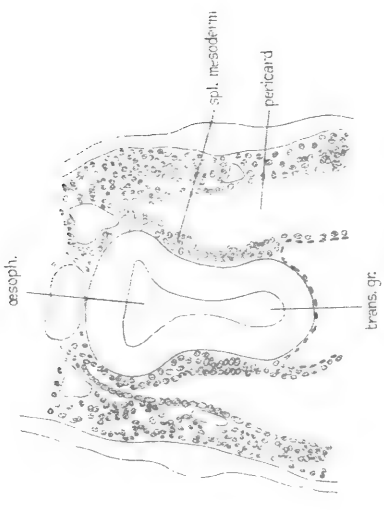

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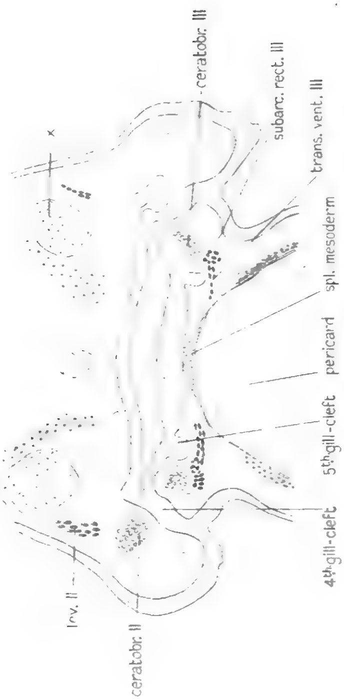

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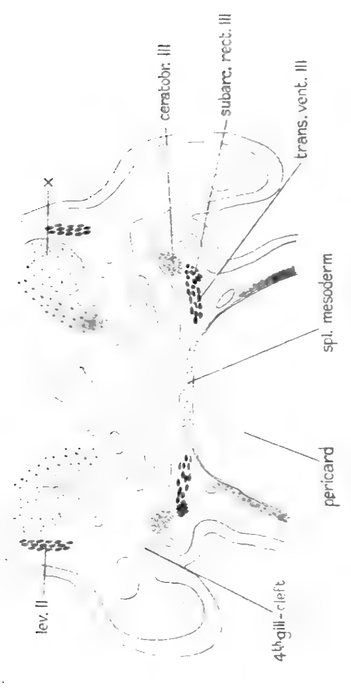

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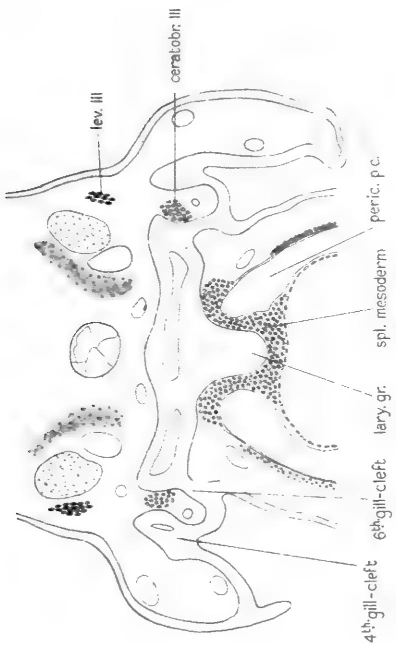

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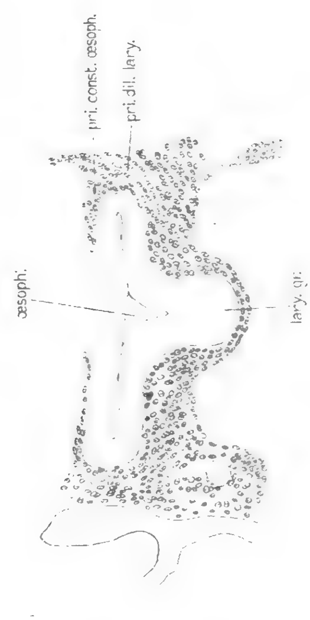

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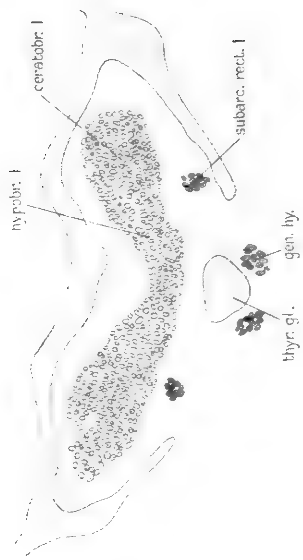

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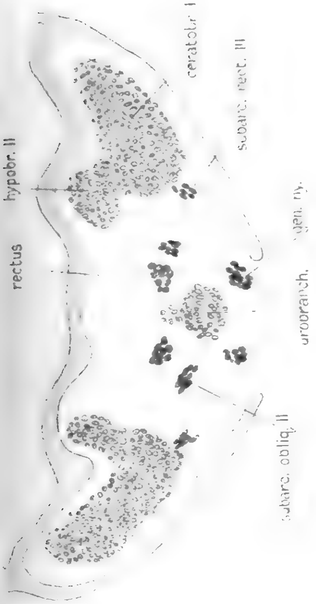

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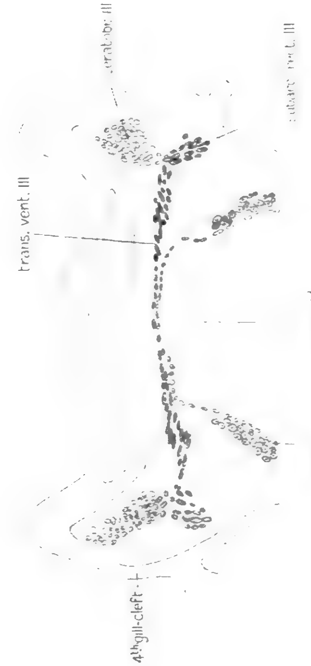

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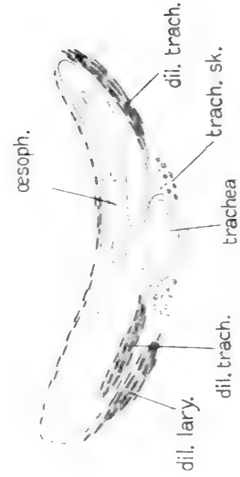

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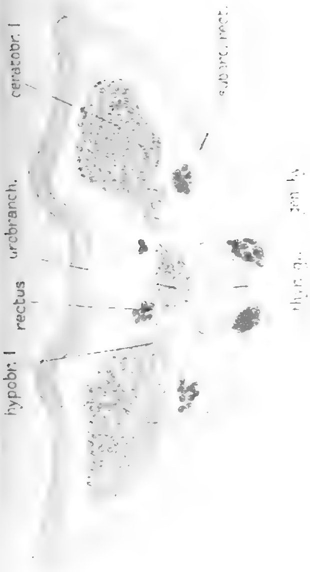

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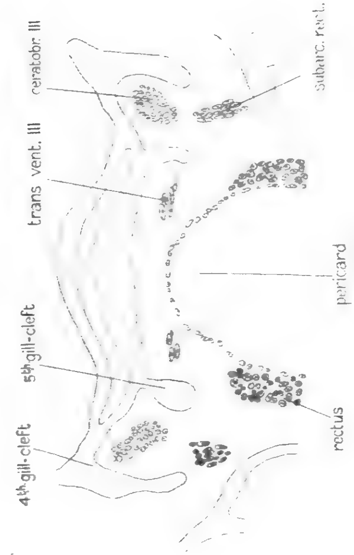

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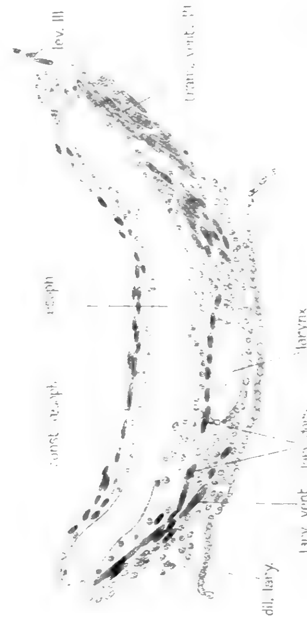

Fig. 69.

const. lary. ...	... M. constrictor laryngis
const. lary. post.	... M. constrictor laryngis posterior
dil. lary. ...	... M. dilatator laryngis
dil. trach. ...	... M. dilatator trachealis
gen. gloss. ...	... M. genio-glossus
gen. hy. ...	... M. genio-hyoideus
gen. hy. lat. ...	... M. genio-hyoideus lateralis
gen. hy. med. ...	... M. genio-hyoideus medialis
Göppert's m. ...	... muscle described by Göppert
hyophary. int....	... M. hyo-pharyngeus internus
hypobr. pl. ...	... hypobranchial plate
inter. hy. ...	... M. interhyoideus
intermand. ...	... M. intermandibularis
lary. dors. ...	... M. laryngeus dorsalis
lary. vent. ...	... M. laryngeus ventralis
lary. gr. ...	... laryngeal groove
Lev.	... M. Levator arcus branchialis
Marg. i ...	... M. marginalis of first branchial bar
oesoph. ...	... oesophagus
omo-hum.-maxillaris ...	M. omo-humero-maxillaris
pars lary. c. l. ...	... pars laryngea cartilaginis lateralis
pericard. ...	... pericardium
peric. p. c. ...	... pericardio-peritoneal canal
pri. annulus ...	... primordium of annulus
pri. aryten. ...	... „ arytenoid cartilage
pri. const. oesoph.	... „ M. constrictor oesophagi
pri. dil. lary. ...	... „ M. dilatator laryngis
pri. hypobr. sp. m.	... „ hypobranchial spinal muscles
pri. proc. trach.	... „ processus trachealis
rec. intest. n. ...	... N. recurrens intestinalis
rect. superf. ...	... M. rectus superficialis
subarc. obl. ...	... M. subarcualis obliquus
subarc. rect. ...	... M. subarcualis rectus
thyr. gl. ...	... thyroid gland
trans. gr. ...	... transverse groove
trans. vent. ...	... M. transversus ventralis
tend. of rect. ...	... tendon of M. rectus
vent. aor. ...	... ventral aorta
vent. pr. basibra.	... ventral process of first Basibranchiale
urobranch. ...	... Urobranchiale

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CARDIAC AND GENITO-URINARY ANOMALIES IN THE SAME SUBJECT

By ALEXANDER BLACKHALL-MORISON, M.D., F.R.C.P.
and ERNEST HENRY SHAW, M.R.C.P.

F. S., male, 38 years of age, was admitted into the Great Northern Central Hospital on March 6, 1919. The previous history obtainable was of "heart-trouble" for three years and "pain in the head" for four weeks. Two nights previous to admission, the headache was severe and on awaking from sleep, ptosis of the left upper eyelid was observed. There was also a history of a severe cold with cough and some haemoptosis in 1916.

On March 7, the mental condition is noted as having been "strange" and the patient is stated to have become cyanosed at times. On the 8th he is described as "deranged," restless and complaining of headache. The heart examined at this date is stated to have shown a loud, "flapping" first sound and a systolic bruit not conducted outwards to the left. The pulse rate is stated at the same time to have been "slow," regular and feeble. There was complete oculo-motor paralysis of the left eye, but no motor or sensory disturbance was notable elsewhere. There was some stiffness of the left leg and an exaggerated knee-jerk in the same limb. The urine was free from albumin and sugar.

On March 10th signs of intracranial pressure were marked and the visiting physician examined him on the afternoon of that day. The patient was found to be delirious and incapable of answering any questions. The oculo-motor signs described were well-marked. On examining the heart, one was struck by the peculiarity of the auscultatory signs. The apical systolic bruit was not audible in the left paravertebral groove and so marked was the accentuation of the first sound, that it could be described by no other term than as a *loud smack*. The condition of the patient precluded more detailed examination and he died the same day.

On *post mortem* examination, the deceased was found to have tuberculous meningitis, and the lungs showed several small cavities at the pulmonary apices and scattered tuberculous foci in the lower lobes. The heart and genito-urinary organs showed abnormalities to be described more fully. The following description of the heart is given by Dr Alexander Blackhall-Morison:

The *right ventricle* is dilated and hypertrophied, the thickest portion of the wall having a diameter of 5 cm. The chamber measures 9 × 7 cm. The columnae carneae are decidedly hypertrophied and especially so is the mass running downwards and outwards from the base of the posterior cusp of the

pulmonary arterial valve (Pl. XVI, fig. 1). These cusps are themselves normal. The transverse measurement of the pulmonary artery is 6 cm. The endocardium below the pulmonary valves is opaque. The tricuspid orifice is dilated, easily admitting three fingers and measuring 5 cm. transversely and the same antero-posteriorly. The internal or septal cusp is fleshy, sessile and of no valvular value. The *anterior cusp* measures 4 × 5 cm. and is attached in its normal position. The *posterior cusp* at its right boundary coalesces with the right limit of the anterior cusp, but is attached abnormally low in the ventricle and its left portion is divided into two pieces. A large, tough, umbrella-like flap is attached to the ventricle close to its apex and a second smaller portion is, like the internal cusp, fleshy, sessile and of no valvular value. The *right auricle* measures 8 × 6 cm. and is hypertrophied. This chamber is also dilated. The *foramen ovale* and venous entrances are normal and the *coronary sinus* is provided with a well-developed Thebesian valve.

The *left auricle* is normal, as usual opaque in lining and smooth in surface.

The *left ventricle* measures 7 × 6 cm. and its wall at its thickest 2 cm. The mitral and aortic cusps are normal. The *mitral* orifice measures 7½ cm. transversely and the *aortic* orifice 5 cm. There are two coronary arteries and the base of the aorta is slightly atheromatous.

The anatomical point of chief interest in the cardiac conditions described, as bearing upon clinical diagnoses, has reference to the abnormal tricuspid segments. The very strikingly exaggerated loudness or accentuation of the first sound of the heart was manifestly due to the impact of blood in systole upon the redundant tricuspid segments. The effect reminded one of the sudden slap of a loose sail rendered taut by a gust of wind. The great audibility of the sign may also in a less degree have been due to the superficial position of the ventricle affected, for, dextral signs caused by organic valvular disease are for this anatomical reason more pronounced than those arising in the deeper left ventricle. An indirect anatomico-physiological interest likewise attaches to this case as elucidating the chief cause of the accentuated first sound in mitral stenoses. Of this a variety of explanations has been offered, but this case strongly supports the view that that diagnostic sign is chiefly attributable to the impact of ventricular blood in systole on the more or less fixed aortic segment of the mitral valve. Dr Ernest Henry Shaw gives the following description of the genito-urinary anomalies in the case:

Congenital absence of one kidney with abnormal development of ureter of same side (fig. 2).

The specimen consists of the bladder with the vesiculae seminales and portions of the vasa deferentia, and the malformed ureter of the left side. The bladder is normal in size and its wall is natural in thickness. Internally a rounded prominence is seen to the left of the trigone about ¾ in. in diameter. It is formed by a thin layer of tissue which is easily depressed by the finger into a large sac in and behind the bladder wall. No ureteral opening is visible on the left side. A ridge of firm muscular tissue runs down from the promi-

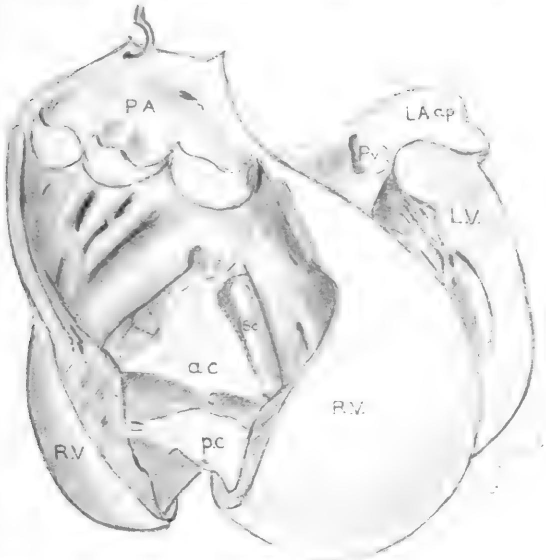


Fig. 1. R.V. right ventricle. P.A. pulmonary artery. S.c. septal cusp of tricuspid valve; a.c. anterior cusp and p.c. posterior cusp of the same. L.V. left ventricle. P.v. pulmonary vein. L.A.ap. left auricular appendix.

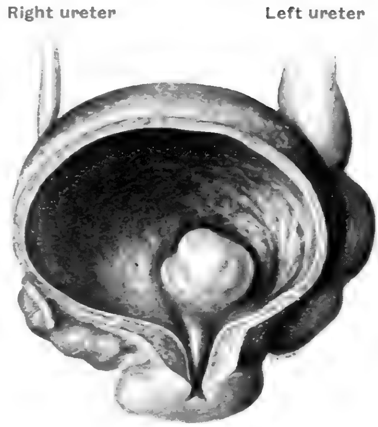
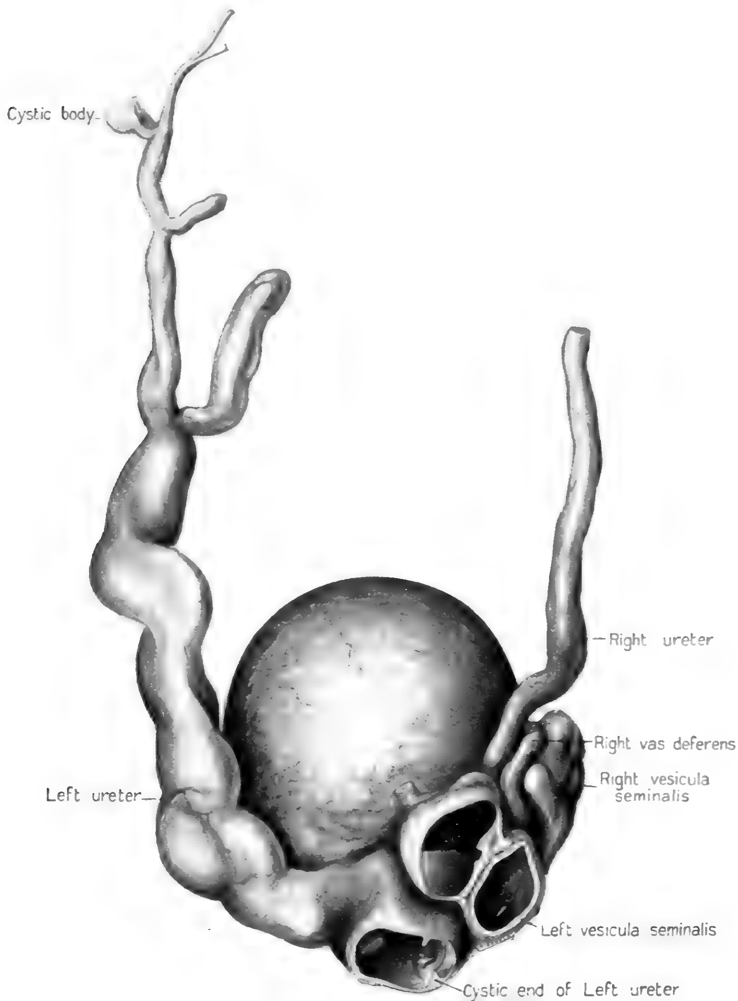


Fig. 2.



nence and becomes continuous with the verumontanum. The orifice of the right ureter is seen in its usual position and is natural in size.

On the posterior aspect a large sacculated cavity is seen in the left wall of the bladder and from this the ureter emerges. The left seminal vesicle is large and dilated to form a bilobed cyst, at the bottom of the cyst a rod is passed through a small hole into the large cyst at the lower end of the ureter. The left vas is much dilated below and then suddenly contracts to a narrow hollow rod as it enters the base of the prostate.

The left ureter begins below as a large thin walled sacculated tube which runs upwards in a convoluted manner and gradually becomes narrower. Towards the upper end it gives off a narrow branch about two inches long and further up a second branch about one inch long. Both branches are hollow and end blindly. The ureter ends above in a small cystic mass and from the upper part of this two strands of tissue taper away.

The vesiculae seminales and vas deferens on the right side are natural. The ureter is a little enlarged.

The left ureter was filled with turbid yellowish fluid which contained many cells of various shape and size, granular material, and a large number of spermatozoa. The latter were mostly small and ill-formed, but many were quite normal in size and shape. On injecting formalin solution into the dilated ureter it first passed into the left seminal vesicle which became distended, it then issued from the cut end of the vas deferens. A channel of communication between the ureter and vas was thus clearly proved. The hole between the ureter and seminal vesicle suggests that the channel is linked up by this organ. There is no communication between the left ureter and the bladder cavity.

The small cystic mass at the upper end of the ureter may represent a rudimentary kidney. Microscopically the cysts and some small tubes are lined with columnar epithelium.

The right kidney weighed 15 oz. and appeared to be normal.

The specimen appears to be valuable from a developmental point of view. It supports the theory of the origin of the ureter being formed by an offshoot from the Wolffian duct (vas deferens). The lateral branches of the upper part suggest the formation of the calicyes found in the normal kidney. The dilatation of the ureter is due to pressure by the accumulation of seminal fluid, and the tube may be said to form a huge seminal vesicle. The formalin solution did not escape from the ejaculatory duct and it is not possible to tell from the present state of the dissection whether this tube is present or if it is patent.

ON THE PARATHYREOID DUCT OF PEPERE AND ITS RELATION TO THE POST-BRANCHIAL BODY

By Dr MADGE ROBERTSON,

From the Physiological Laboratory, University of Glasgow

In certain mammals the extraordinary mixture of the thyreoid with the organs developed from the gill clefts and of these with one another has led not only to misunderstanding of the results of physiological experiments, but also to confusion in the interpretation of the morphological relationships of the various structures.

The elaborate paper by Mrs F. D. Thompson (*Phil. Trans.* B, vol. 201) illustrates this from the morphological side, while the earlier conclusions of Swale Vincent and of Forsyth on the functional identity of thyreoids and parathyreoids indicate the danger from the physiological aspect (Alnason and Swale Vincent, *Transactions of the Royal Society of Canada*, 1917, p. 121).

In the cat the mix-up is very striking. Not only are the two ordinary parathyreoids found in connection with each lobe of the thyreoid but thymus tissue is generally present in close relation to both, while parathyreoid nodules occur in the thymus in about 50 per cent., according to the observations of Harvier.

The development and structure of the thyreoid, parathyreoid and thymus have been very fully investigated but the relation and significance of the post-branchial body in mammals are still obscure.

The structure seems to have been first observed by Sandström when he described the parathyreoids. Pepere (*Arch. Ital. de Biol.* 48–49) calls it the "parathyreoid duct," although as will be shown it is not necessarily connected with these structures.

In the routine study of a large series of thyro-parathyreoid structures removed from cats and dogs by Professor Noël Paton and Dr Leonard Findlay in their investigation on Tetania Parathyreopriva (*Q. J. of Exp. Phys.* vol. x. p. 203, 1917) and of several thymus glands the presence of a structure closely corresponding in character with this post-branchial body has been found in connection with the parathyreoid and thymus nodules of the thyreoid and also in the thymus.

The tissues were fixed in picro-formalin, cut serially in paraffin and stained in haemalum and eosin.

In 33 cat thyreoids examined in serial section I found it present in all, while in the thyreoids of 11 dogs it was found in 8.

In the thymus glands of two dogs and one cat systematically examined a similar structure was present.

This body varies greatly in size, shape and character. It is essentially of the nature of a multi-loculated cyst, with duct-like channels extending from it in various directions.

Generally part of it lies deep in the thyreoid, and it here frequently has the appearance of a much enlarged thyreoid vesicle, filled, not with the pink staining colloid of the thyreoid, but with a homogeneous material staining of a blackish blue colour.

At other parts the walls are thicker, with more fibrous tissue around them, and they form partial septa giving a multi-loculated character.

The epithelial lining shows marked variations. Sometimes a single layer of flattened epithelium is present, sometimes the cells are columnar and sometimes they are ciliated (Plate XVII, Fig. 1). Sometimes there are several layers of horny-looking flattened cells, which occasionally completely fill the lumen. In many of the loculi and channels this epithelium can be seen breaking down and becoming necrotic often forming a mass of homogeneous debris (Plate XVII, Figs. 2, 3, 4).

Certain features are common to the duct in all its forms.

(1) The channels have origin in the breaking down of epithelial cells of a type quite distinct from those of the parathyreoid and thyreoid and easily recognisable in the midst of either of these. The epithelial cells of the "duct" are larger than those of the thyreoid or parathyreoid, they stain as a rule more faintly, and they are sometimes peculiarly clear and almost refractile in appearance.

(2) There is associated always with the ducts at some stage of their course, and frequently throughout the whole of their course, a greater or less amount of lymphoid tissue closely resembling thymus. Mixed with the round lymphoid cells are many spindle shaped cells such as have been described by Dudgeon (*Journal of Path. and Bact.* 1905, p. 173) as occurring in the thymus in atrophy.

(3) The duct-like structures are almost always in some part of their course in close connection with one or other of the parathyreoids.

(4) They contain a large amount of homogeneous necrotic material obviously derived from broken down epithelial cells, and differing, as a rule, in its staining properties from the colloid of the thyreoid vesicles.

(5) They all appear to end blindly, and must therefore be closed sacs—smaller or greater—and not ducts.

(6) The tissue round about them is not specially vascular and they do not seem to come into any very close relationship with blood vessels.

In the thymus a similar structure repeats all the variations which it showed in the thyreoid. An epithelial lining of tall columnar cells with a very definite basement membrane is however more frequently seen, and sometimes the lumen of the duct is filled with lymphocytes or the products of their degeneration rather than with epithelial cells.

In one case this structure occupied a considerable part of the atrophic thymus and showed the most diverse forms of cells in the lumina.

It occurs most often in the fibrous stroma dividing the gland into lobules, or in fibrous tissue towards the periphery of the gland (Plate XVIII, Figs. 1 and 2), but also in the medullary portion of a lobule. Small pieces of parathyreoid tissue are sometimes seen in the neighbourhood of the duct. Parathyreoid tissue was found in two out of the four thymus glands examined complete (one dog and one cat).

The most interesting feature of the duct in the thymus is the fact that Hassall's corpuscles can be seen quite definitely to be budded off from the epithelium of its walls (Plate XVIII, Figs. 3 and 4) and they frequently form the terminations of some of its loculi.

This structure is so distinctive and so different from the parathyreoid or thymus tissue lying near it that its independent nature is strongly suggested. It is of course possible that it is derived from the degeneration of the epithelial connection of these two structures with the gill clefts, but on the other hand its close resemblance to the post-branchial body as described in elasmobranchs, urodela, frogs, reptiles and birds by Mrs Thompson (*loc. cit.*) strongly suggests its identity with this.

In *Chrysemys Picta* she describes it as follows: "It is in close relation to the parathyreoid. It consists of a number of vesicles of varying size and shape though they tend to be spherical. The vesicles are of two distinct types, some large, with very low epithelium staining very deeply—others smaller, with cylindrical epithelium. Some of the vesicles contain a material which appears to be true colloid."

In birds the post-branchial body is described as consisting of three parts—the first composed of compact epithelial cords, the second of spherical vesicles lined with cubical epithelium which may be ciliated, and the third of true parathyreoid tissue and thymus.

In the pigeon she says "the post-branchial body has an extraordinarily complicated structure. It is obviously of epithelial origin and nature. It is composed largely of structures which at first sight resemble small arteries but whose walls are made up entirely of concentrically placed spindle shaped cells, and projecting into the lumen are irregular cells lining the tubules. The rest of the body appears to be built of structures identical with the various well known forms of Hassall's corpuscles of the thymus."

In the fowl, she says "the post-branchial body is represented by a group of 8–10 vesicles lined with a low cubical epithelium, embedded in a constricted off-portion of the elongated thymus. In the thymus nodule there is also a structure which must be put in the same category. This is a much infolded vesicle of large size lined with columnar ciliated epithelium."

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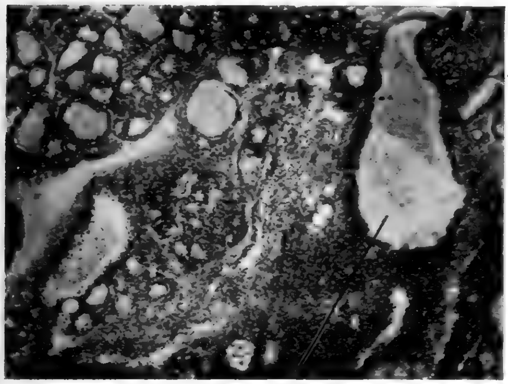


Fig. 1. Duct lined in part with columnar ciliated epithelium. ×100.

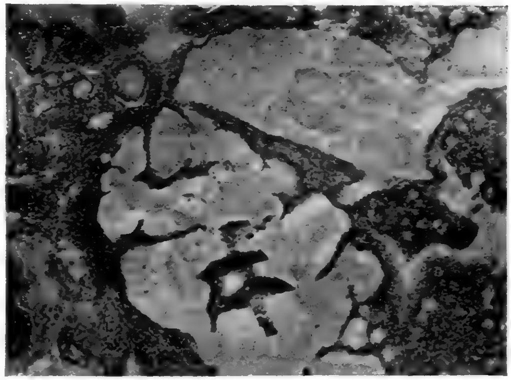


Fig. 2. Very large thin walled duct loculi. ×100.

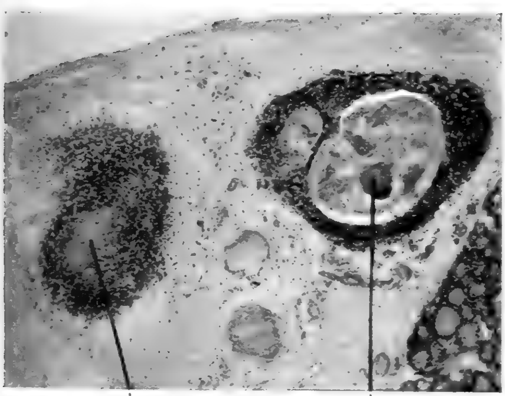


Fig. 3. Epithelial cells. Duct channel filled with homogeneous epithelial debris. ×100.

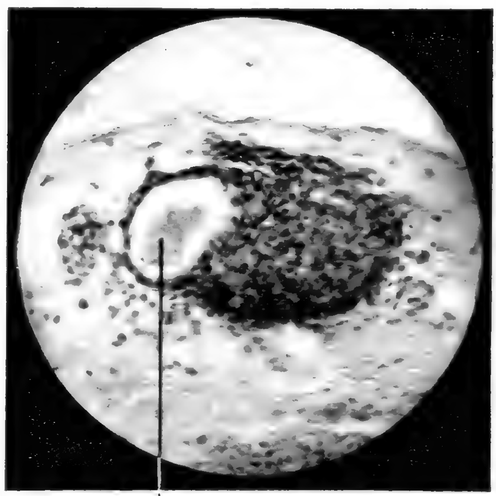


Fig. 4. Well defined duct channel containing some epithelial debris. ×300.

SUMMARY

1. There is in the thyreoid, parathyreoid and thymus glands of cats and dogs a structure cyst-like in some of its forms, and duct-like in others and often of considerable complexity.

2. In a series of 33 thyreoids of cats examined in serial section this structure was found to be present in all. In all thyreoids of dogs examined serially it was found in all but three.

In four thymus glands—three dogs and one cat—examined in serial section it was present in three—two dogs and one cat.

3. The lumen of the structure appears to be formed by the breaking down of large epithelial cells. Sometimes in the thymus it seems to be formed rather by the disintegration of lymphoid cells.

4. By the breaking down of these cells, epithelial and lymphoid, a homogeneous material is formed frequently filling the duct channels and loculi. This material sometimes stains pink with haemalum and eosin like the colloid of the thyreoid vesicles, but more frequently takes a dark bluish black colour.

5. The structure corresponds very closely in appearance with the "post-branchial" body described in fowls and pigeons (and various lower animals) by Mrs F. D. Thompson, and it is suggested that it may be the representative of this body.

6. Hassall's corpuscles can be definitely seen to be budded off from the epithelium forming the duct walls.

I desire to express my thanks to Professor Noël Paton for much kind assistance in the preparation of this paper.

The work was done under a grant from the Medical Research Committee to which my thanks are due.

DESCRIPTION OF PLATES

Plate XVII

Fig. 1. Duct lined in part with ciliated epithelium.

Fig. 2. Very large, thin walled, duct loculi.

Fig. 3. Duct channels developing in lymphoid nodes in capsule of thyreoid by breaking down of epithelial cells.

Fig. 4. Duct channel in capsule of parathyreoid containing degenerating epithelium.

Plate XVIII

Fig. 1 and 2. Duct in fibrous tissue capsule of thymus.

Fig. 3. Duct in centre of thymus lobule. Hassall's corpuscle forming by proliferation of cells of wall. Lymphocytes and epithelial cells in lumen of duct.

Fig. 4. Duct in centre of thymus lobule. Hassall's corpuscle budded off at lower corner of duct channel.

NOTE ON ABNORMAL MUSCLE IN POPLITEAL SPACE

By Prof. F. G. PARSONS

Prof. Parsons showed, at the December Meeting of the Anatomical Society, an abnormal muscle, in the roof of the popliteal space, of which an illustration is given. It was supplied by the external popliteal nerve and

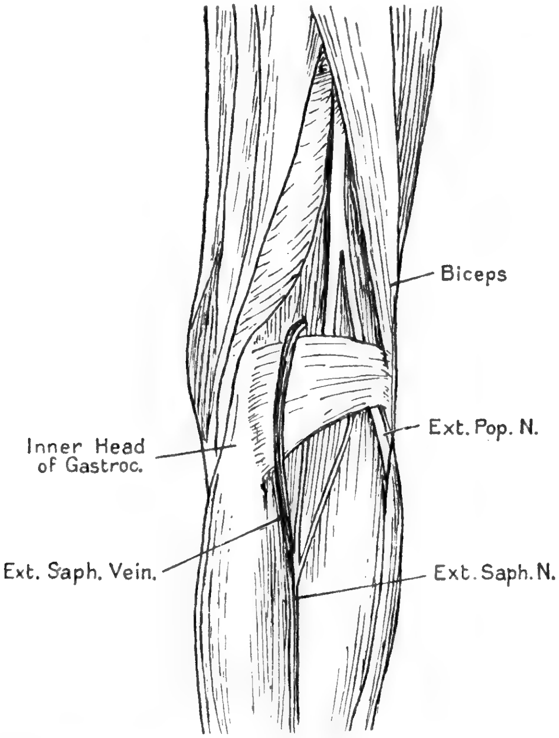


Fig. 1. Dissection of popliteal space showing abnormal muscle described in the text.

Prof. Parsons was inclined to regard it as a conversion of the fascia lata of the thigh into muscle, especially as he had noticed that most of the fibres of the fascia in that region run transversely. He produced specimens to show that other structures which are usually fibrous may be converted into muscle.

LEVEL OF EXTERNAL AUDITORY MEATUS

By Prof. F. G. PARSONS

The accompanying dioptographic tracings of the relation of the external auditory aperture in the soft parts to the bony external auditory meatus were shown by Prof. F. G. Parsons in order to help the solution of the problem as to the allowance which should be made for the soft parts when the auricular height of a skull is taken.

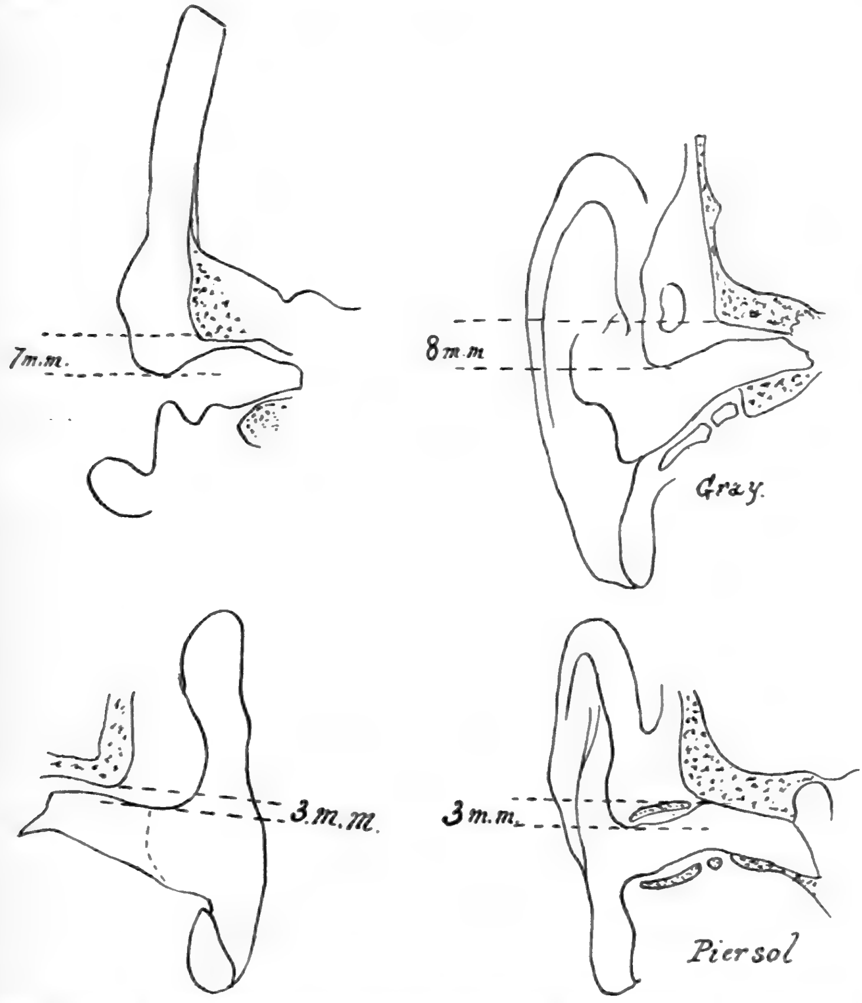


Fig. 1. Vertical coronal sections of the external auditory meatus to show variations in the relationships of the soft parts to roof of meatus.

The four tracings showed that the skin opening is always below that in the bone, but that its distance below varies from 3 to 8 mm.

Until further material is available it will, therefore, be wise to allow an average of 5 mm. for the lower level of the soft meatus, and 4 mm. for the thickness of the scalp on the vertex of the head.

NOTE ON RECURRENT LARYNGEAL NERVES

By Prof. F. G. PARSONS

Prof. F. G. Parsons showed, at the December Meeting of the Anatomical Society, some dissections of the recurrent laryngeal nerves which he had been asked to make by some of the surgeons of St Thomas's Hospital. The points to which he drew special attention were (1) that the nerve, especially on the right side, does not lie in the groove between the trachea and oesophagus, but some little distance away, and may therefore be met with sooner than the operator expects.

(2) That the nerve on the left side gives off a very large branch to communicate with the cervical sympathetic.

(3) That on reaching the thyroid gland the nerve is very closely applied to the posterior part of the internal surface of that structure, lying between it and the trachea and, higher up, between it and the cricoid cartilage. So closely is it attached to the irregular surface of the gland in this region and so obscured is its course just here by arteries and lymphatic glands that the complete removal of the gland without injuring it must be a task of the greatest difficulty.

The relation of the nerve to the inferior thyroid artery is unreliable. A little distance below the gland the main inferior thyroid artery usually passes behind the nerve, just as it passes behind the sympathetic, though this relation is not constant to either structure. When the gland is reached the nerve often becomes the most posterior structure, passing between branches of the artery. The specimens incidentally showed that the right recurrent laryngeal nerve has only a course of about three inches.

HYPERTROPHY OF THE INTERSTITIAL TISSUE OF THE TESTICLE IN MAN

By T. RUSSELL GODDARD

INTRODUCTION

At the time of the outbreak of war I was engaged in Cytological research upon the germ cells. Col. C. J. Bond, C.M.G., F.R.C.S., knowing this, very kindly supplied me with a number of retained testicles, removed by operation from young men who presented themselves for enlistment in His Majesty's Forces.

After a preliminary examination of the slides made from this material, it occurred to me that a comparison of the interstitial tissue found in these organs, with the same tissue in the normal organ in advanced age, might be interesting and perhaps illuminating. It appeared possible that such a comparison might supply some further points of interest having a bearing upon hypertrophy of interstitial tissue, in relation to atrophy of the seminal epithelium.

Shortly after this time I myself joined the army, and consequently the work of examination and preparation of this paper have been delayed until now.

MATERIALS AND METHODS

My material consisted of five retained testicles removed by operation from young men whose ages ranged between 19 and 25 years. The organs were found in various positions above the abdominal ring. In all cases they were smaller than the normal testicle; three of them were roughly about the size of a blackbird's egg, one somewhat smaller, whilst the fifth was nothing more than a collection of gland tissue along the vas deferens and seminal ducts. Immediately after removal they were fixed in Bouin's Picro-Formol, first being opened with a scalpel to allow easier access of the fixing fluid. After remaining about 18 hours in the Picro-Formol, they were washed out in 70 per cent. alcohol, and then transferred to 80 per cent. alcohol. The material was then passed through 90 per cent. alcohol, absolute alcohol, cedar-wood oil, xylol, and embedded in paraffin wax having a melting point of 52° C. Serial sections were cut 8μ thick on an ordinary Cambridge Rocking Microtome. The sections were stained on the slides by Heidenhain's Iron-Alum Haematoxylin, and alcoholic eosin was used as a plasma stain.

I also secured at the same time two normal testicles for comparison and control, one from a boy aged 17, and the other from an old man aged 78. In the case of the boy the organ was removed and fixed in Bouin's Picro-Formol, a few hours after death. In the case of the old man the organ was removed

by operation, and preserved in 7 per cent formol. The methods employed in making the slides were the same as those used in the case of the retained organs.

THE RETAINED TESTICLES

General Description

Each testicle is invested with a tunica albuginea of normal thickness. The seminiferous tubules are as numerous as they are in the normal organ, but their diameter is somewhat smaller. Large intertubular areas of fibrous stroma are quite infrequent, the organs usually being tightly packed with seminiferous tubules. The individual organs examined vary slightly in this respect.

The seminiferous tubules in no instance exhibit any signs of spermatogenesis. The seminal epithelium in all cases is atrophied, the tubules being tightly filled with degenerating cells. The size and shape of these cells and their nuclei vary slightly in different individuals. In some cases the cells are roughly spherical, and in these the nuclei are also spherical. In others, the cells and their nuclei are elliptical. The cytoplasm is clear and very finely granular.

Interstitial Tissue

In all the retained organs examined, the interstitial tissue is found to be extremely well developed. In fact, more so than in the normal organ during active spermatogenesis. Large areas are found in the intertubular stroma, which are tightly packed with the cells of Leydig, more commonly known as interstitial cells. These cells are large and irregular in shape, the cytoplasm is clear and finely granular, and stains strongly with eosin. Lying in the cytoplasm near the nucleus is usually a well-defined attraction sphere containing a double centrosome. The nucleus is large and spherical, having a sharply-defined nuclear membrane. One, two, or three large and deeply staining chromatic nucleoli are found, and scattered irregularly throughout the linen meshwork are numerous chromatin granules. Occasionally a plasmosome is present.

NORMAL TESTICLE (Man *aet.* 78)

General Description

The seminiferous tubules are not so numerous, and are more widely separated by interstitial tissue, than is the case in the organs from young men. The testicle is well supplied with blood vessels. The tubules are lined with seminal epithelium, but present marked signs of decreased activity. The majority of the cells are primary spermatocytes in the resting stage. Many of the cells are atrophied, and present an appearance similar to that of the cells found in the seminiferous tubules of the retained organ. Spermatozoa are found in some of the tubules.

Interstitial Tissue

Large areas are met with between the tubules, which are tightly packed with interstitial cells. The nuclei are large and take the stain deeply, having

a sharply defined nuclear membrane. They contain one, two, or three large nucleoli, and numerous chromatin granules dispersed irregularly throughout the linen meshwork. Occasionally oxyphil granules are present. Most of the cells contain an attraction sphere enclosing a double centrosome. The cytoplasm is finely granular and stains deeply with eosin. All the interstitial cells observed show pronounced signs of activity. The shape of the cells appears to be arbitrary, and dependent upon how tightly packed they are in the intertubular tissue. The interstitial cells are much more numerous in this testicle than they are either in the normal testicle from the boy, or in the retained organs. Large areas tightly packed with them are frequently observed.

SUMMARY

1. In all the retained organs examined, there was complete atrophy of the contents of the seminiferous tubules.
2. In all cases there was a marked hypertrophy of the interstitial tissue, in some instances more pronounced than in others.
3. In the case of the normal testicle removed by operation from the old man aged 78 years, the contents of the seminiferous tubules exhibited signs of diminished activity.
4. The interstitial tissue of this organ exhibited a very pronounced hypertrophy.

CONCLUSIONS

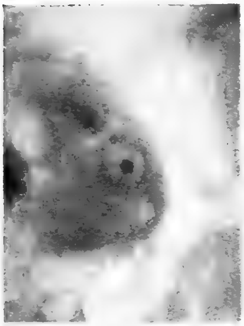
The first part of this paper, that relating to the retained testicles, corroborates the work of other observers. The latter part dealing with the condition of the interstitial cells in old age in man, is, so far as I am aware, new and interesting. It is unwise, to say the least, to formulate any hypotheses upon the evidence of one individual. However, I intend to carry out further investigation upon the subject, and by examining a number of testicles from old men, I shall be able to decide whether this condition is normal in advanced age or not. If this condition is normal, it seems highly improbable that the increased activity of the interstitial cells has any connection with an increased development of secondary sex characters. Rasmussen has apparently found a parallel case in the rodents. In a paper published in 1917 he states that in the Woodchuck (*Marmota monax*), which is sexually active only in the spring, interstitial cell growth seems more uniformly related to the later and regressive stages of spermatogenesis, than to the initial stages. However, he says that there is evidence of variability even in regard to these. On the other hand, Tandler and Grosz have shown that in other animals which undergo seasonal changes in sexual activity, increased development of interstitial cells immediately precedes that of the seminal epithelium. However, from the work that has been done upon the subject, it appears usual to find increased activity of the interstitial cells when the seminiferous tubules are either decreasing in activity, or completely inactive. In addition this condition has been produced experimentally by ligature of the vas deferens. It appears

that the seminal epithelium and the interstitial tissue are closely inter-related, and that increased activity of the latter is influenced by diminished activity or atrophy of the former. For what physiological reason, in the existing state of our knowledge, it seems impossible to decide. It cannot in all cases mean an increased secretion of hormones.

DESCRIPTION OF PLATE XIX

Figures 1 to 6 are from photomicrographs made with a Zeiss camera, a Zeiss apochromatic oil-immersion objective of 2 mm. focus and N.A. 1·30, and compensating ocular No. 4. The light was obtained from a Graetzin lamp and passed through a Watson holoscopic oil-immersion sub-stage condenser. Figures 7 to 9 were photographed through a Zeiss A objective of $\frac{3}{4}$ in. focus and N.A. ·20. In all cases the camera extension was 50 cm. The magnification was obtained from a stage micrometer graduated to read one-hundredth parts of a millimetre. Photographs of this scale were taken under both combinations and are included in the plate.

Fig. 1. Interstitial cell from normal testicle (Boy *aet.* 17).
Fig. 2. *Idem.* Nuclei as large as this are rare in this testicle.
Fig. 3. Group of Interstitial cells from one of the retained testicles.
Fig. 4. Interstitial cells from retained testicle. A double centrosome will be seen lying in the cytoplasm below the nucleus in the centre of the figure.
Fig. 5. Giant cell and nucleus from normal testicle (Old man *aet.* 78).
Fig. 6. Group of Interstitial cells from normal testicle (Old man *aet.* 78).
Fig. 7. Seminiferous tubules from normal testicle (Boy *aet.* 17). Small islands of Interstitial cells are shown between the tubules.
Fig. 8. Seminiferous tubules from one of the retained testicles. The intertubular spaces are tightly filled with Interstitial cells. The contents of the tubules are atrophied.
Fig. 9. Seminiferous tubules from normal testicle (Old man *aet.* 78). Large areas of Interstitial cells are shown between the tubules. The contents of the tubules exhibit signs of diminished activity.
Fig. 10. Photograph of stage micrometer showing magnification of Figs. 1 to 6.
Fig. 11. Photograph of stage micrometer showing magnification of Figs. 7 to 9.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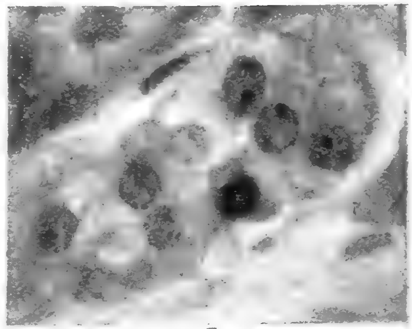
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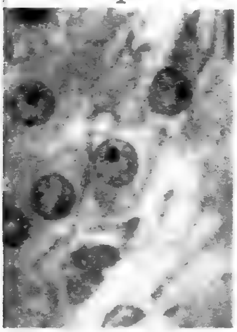
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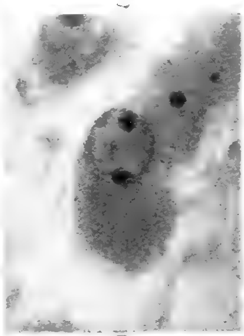
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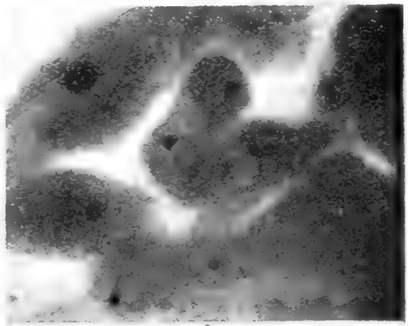
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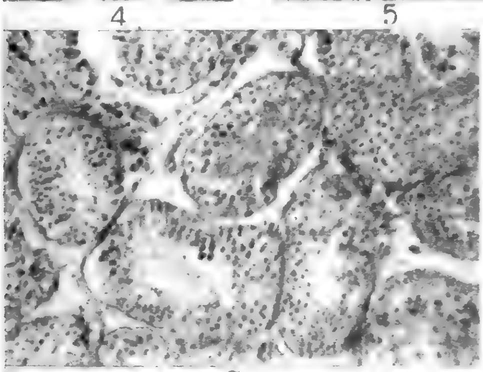
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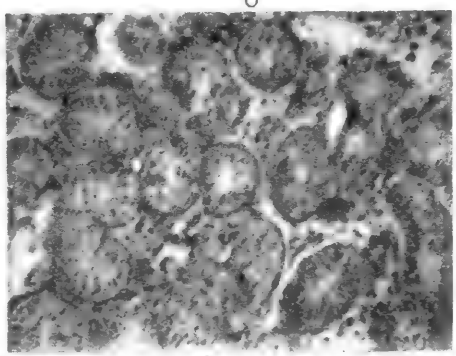
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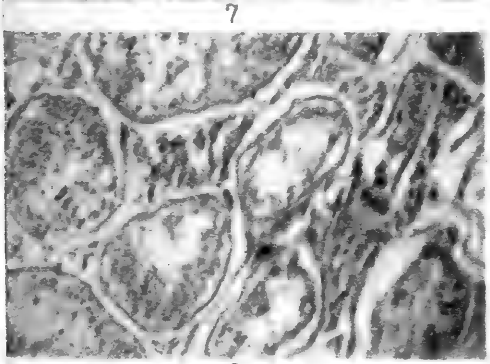
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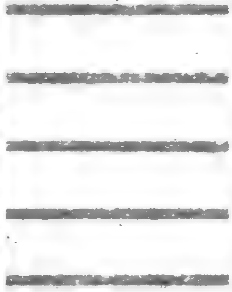
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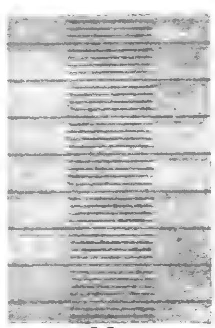
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THE ORA SERRATA RETINAE

By G. F. ALEXANDER, M.B., Ch.B. (Ed.)

The above name is a sadly mistaken one for the serrated border of the Retina, being wrongly in the plural: a better one would surely be Limbus Serratus. But why is the mouth or border of the Retina, i.e. where this membrane ends at the Ciliary Body, serrated? I do not think any explanation has hitherto been forthcoming other than that it "grew so." The Ciliary Body is universally described as consisting of a posterior zone termed the Orbiculus Ciliaris or Pars Plana on account of its being smooth, and an anterior zone bearing the Ciliary Processes or Pars Plicata. The great mistake, however, has been perpetuated in describing the posterior zone as smooth for it is not so, as a careful examination will reveal the following, viz., from the posterior aspect of each Process there continues backwards to the border of the posterior zone a slightly elevated prolongation of its posterior border as a ridge or Subsidiary Process, highest in the centre and tapering on each side into continuity with the flat internal wall of the Ciliary Body, which thus consists of a series of sulci between the elevations given by the Main and Subsidiary Processes. A further interesting feature of the Subsidiary Processes is that each consists of a number of low parallel radial ridges. Now before the Retina ends by the hexagonal pigment cells continuing as the outer layer, and its supporting fibres as the inner layer, of its Pars Ciliaris (the transition of these nucleated fibres into the epithelial cells being the exact counterpart of that of the epithelial cells of the lens capsule into the lenticular fibres), it passes for a short distance over the Orbiculus, and this overlying hem through being raised upwards by the Subsidiary Processes is thrown into a series of elevations and depressions and thus acquires a serrated appearance.

NOTE ON THE OCCURRENCE OF CILIATED EPITHELIUM IN THE OESOPHAGUS OF A SEVENTH MONTH HUMAN FOETUS

By F. H. HEALEY, B.Sc.

From the Physiological Laboratory of the University of Birmingham

During the summer of 1918 a recently dead, well nourished, seventh month, female foetus was sent to the department and appeared perfectly normal. Portions of various organs were removed and fixed in 10 per cent. formalin for class purposes; among these were the oesophagus, trachea and stomach.

The oesophagus was divided transversely into three segments and the cardio-oesophageal junction opened longitudinally, pinned flat on a cork and fixed in that position. The tissues were then treated in the usual way, finally embedded in paraffin and sectioned. Various staining agents were used including haematoxylin, eosine, van Gieson, methyl blue and iron haematoxylin.

On examination it was at once seen that the mucous membrane of the oesophagus presented a remarkable feature, namely, that superimposed upon the usual stratified squamous epithelial lining were patches of ciliated cells varying in extent and in position; sometimes occupying the crests of the folds and sometimes the sulci between them. On the whole they were more numerous in the upper end of the tube than lower down, but some were still visible even to the orifice of the tube into the stomach.

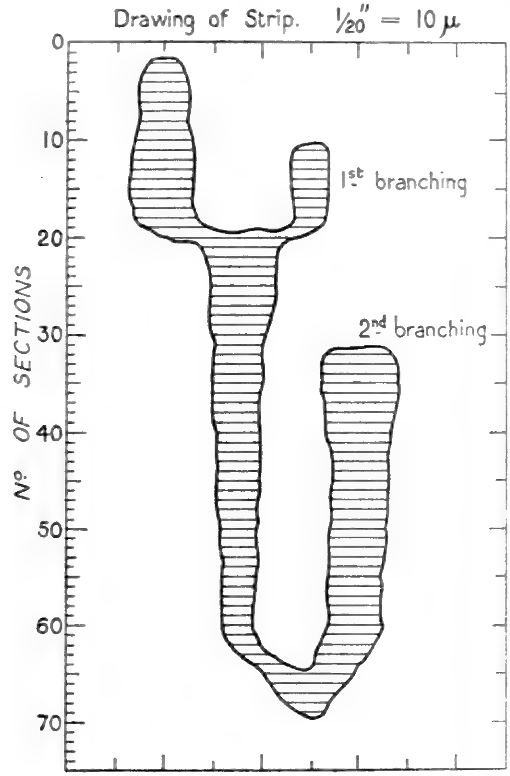
The ciliated patches were well defined and did not project above the general level of the epithelium, the stratified epithelium being pitted to receive them. There was also a marked absence of mucous glands in the submucous coat. Apart from these peculiarities the structure of the oesophagus was quite normal.

The ciliated cells on examination proved to be of the ordinary columnar type, measuring $14{\cdot}5 \times 9{\cdot}8\mu$ and presenting flagellae $6{\cdot}8\mu$ in length. These were implanted upon well-marked basal segments, from which depended the usual rootlets.

To determine the extent of the patches serial sections 10μ in thickness were cut from the middle third of the oesophagus and mounted serially on slides.

Definite patches were selected and their course followed throughout the series. The number of ciliated cells and the breadth of the patch in microns were recorded for each section. By this means the patches were found to run mainly in a longitudinal direction and might be better described as

strips than as patches. They showed branchings and bifurcations at different levels; the branches also had a longitudinal arrangement. Some strips were very short, running through only a few sections, others were of greater length, extending through 60 or 70 sections.



No. of section	Breadth of main part	Breadth of bifurcation
2	30μ	—
8	50μ	—
11	60μ	35·2μ
18	59μ	34·6μ
20	87·8μ	—
	First bifurcation joins main part	
21	74·4μ	—
30	53μ	—
32	55μ	65μ
42	45μ	60μ
50	42·6μ	61μ
60	36μ	69μ
65	94μ	—
	Second bifurcation joins main part	
69	24μ	

Distance between first bifurcation and main part at section 11 = 100μ
,, second ,, ,, ,, 32 = 62μ

The dimensions and configuration of a typical strip are set forth in the preceding table and drawing. It measures 690μ in total length, bifurcates twice, one branch being much longer than the other, and the strip varies in breadth from three to ten cells.

Sections from the trachea of the same foetus were then examined to ascertain whether the ciliated cells might not, by some accident, have been derived from its mucous membrane; but the trachea proved perfectly normal and its epithelium quite unabraided. The cells therefore could not have been desquamated from the air passages. This was done only as a precautionary measure, there being no reason to suppose that they were derived from any other locality, because they were sunk in little depressions in the squamous epithelium and exhibited no dislocation and besides, the cells were quite healthy, without the slightest sign of degeneration.

Examination was next made of the transverse sections of the oesophagus of the following human embryos kindly placed at my disposal by Prof. Peter Thompson of the Anatomical Department:

3 mm. long
5 mm. „
7 mm. „
11·25 mm. long
16 mm. long,

but no trace of ciliated epithelium could be found in the oesophagus of any of them. (I have to thank Dr Yates of the Middlesex Hospital for his kindness in examining the 11·25 mm. embryo for me.)

Sections in the collection in the Physiology Department were also examined, but in none of them could any trace of cilia be found in the oesophagus. They included:

Foetal Sheep
12th day Rabbit embryo
Mouse embryo 1 cm. long
„ 2 cm. „
Bat embryo
Foetal Hedgehog
New born Kitten
5th day Chick.

The condition under examination seems therefore to be a rare one and is not without interest from both an embryological and a pathological standpoint.

Considered embryologically the phenomenon is not so surprising, because the trachea and the oesophagus are developed from the same portion of the primitive foregut, i.e. the part between the developing pharynx proximally and the future stomach caudally;—the oesophagus being the dorsal part of the original tube and the trachea the ventral part. Originally they were both lined by the endoderm of the alimentary canal, but at a later stage, this endoderm in the trachea develops into the ciliated epithelium of the adult, while that of the oesophagus becomes stratified squamous. In the oesophagus of the foetus under consideration, there are strips of ciliated epithelium which

are obviously not disintegrated epithelium from the trachea superimposed on the normal epithelium of the oesophagus, because (*a*) the structure of the trachea is quite normal, the epithelium being intact. (*b*) The strips in the oesophagus are not simply superimposed but are directly continuous on either side with the squamous cells. Hence the question arises as to whether the oesophagus is ciliated normally at an early stage in its development, afterwards losing its ciliated epithelium, such a condition being possible because of the occurrence of epithelioma in the adult oesophagus.

It thus remains to be demonstrated that at an early stage in the development of the oesophagus it is a ciliated tube like the trachea, the embryonic endoderm cells becoming ciliated cells which only persist for a short time, and then disappear entirely, leaving the ordinary squamous epithelium. If this is so, then in the present case only parts of the ciliated epithelium have disappeared, some persisting in the form of strips. But since in no embryo examined could any trace of cilia be found in the oesophagus, its occurrence in this foetus is probably an abnormality, and in the normal development of the oesophagus no ciliated epithelium is ever present.

This foetus is also of interest to the Pathologist. New growths in the adult may possibly be due, in part at any rate, to such abnormalities, which, though perfectly normal low down in the animal scale, only occasionally occur in higher forms and may be looked upon as vestigial remains, which, according to some pathologists, may afford a suitable nidus for the development of cancer and other malignant growths.

THE RELATIVE POSITIONS OF THE OPTIC DISC AND MACULA LUTEA TO THE POSTERIOR POLE OF THE EYE

By JAMES FISON, M.A., M.D. (Cantab.),

Harrogate

Many years ago I noticed in the third volume of L. Testut's *Traité d'Anatomie Humaine* (4e édition) what I at first took to be mere printers' errors in the description of the macula lutea and the optic disc. They occur in the following passages:

"La tache jaune...occupe exactement le pôle postérieur de l'œil. Elle est située par conséquent un peu en dehors et un peu au-dessus de la papille optique."

"Elle (la papille optique) revêt l'aspect d'un petit disque...située à 3 millimètres en dedans, et à 1 millimètre au-dessous du pôle postérieur de l'œil."

I soon saw, however, that this was not a misprint of "au-dessous" for "au-dessus" and *vice-versâ*, for in three illustrations (one of them a coloured plate) the macula is shown above the level of the centre of the optic disc. The coloured plate bears the legend: "La rétine, vue à l'ophthalmoscope, œil gauche, image droite." In reality it shows the reversed image of the right eye. In the description of the sclera the following passage occurs: "Elle (l'ouverture postérieure) est située à 3 millimètres en dedans et à 1 millimètre au-dessous de ce pôle (pôle postérieur)"; and in a figure, showing the back view of the eye, the entrance of the optic nerve is placed well below the horizontal meridian.

In the latest edition of Testut and Jacob's *Traité d'Anatomie Topographique* some corrections have been made. The description beneath the coloured plate—the same plate as that found in the *Traité d'Anatomie Humaine*—is as follows: "La choroïde et la rétine vues à l'ophthalmoscope, œil gauche, image renversée." Here the correction has not gone far enough, for it is a reversed image of the right eye that is represented and not the left. But in subsequent figures of this region, in all of which the macula lutea is on a higher level than the optic disc, there is no mention of the reversed image.

In the text the optic disc is described as being "à 3 millimètres en dedans et à 1 millimètre au-dessus du pôle postérieur de l'œil," and the macula "qui occupe exactement le pôle postérieur de l'œil" as being "un peu au-dessous de la papille." But, when the sclera is under consideration, Testut states that the posterior opening of the sclera is "à 3 millimètres en dedans et à 1 millimètre au-dessous de ce pôle (pôle postérieur)," and the figure on the same

page (the same as that in the *Traité d'Anatomie Humaine*) bears out this wrong description.

If such inconsistent statements and inaccurate illustrations could be found in Testut's works I expected to find other anatomists also at fault in their articles on the Eye; for Testut is justly regarded as one of the greatest living anatomists, and his works are not infrequently referred to in English treatises on Human Anatomy and Surgical Anatomy. In the eleventh edition of Quain's *Elements of Anatomy*, in three separate passages, the head of the optic nerve is said to be on a lower level than the horizontal meridian of the eye. One of these passages reads as follows: "About 3 mm. inside the yellow spot and about 1 mm. below the level of a horizontal line through the posterior pole of the eyeball is...the optic disc." Two figures show the macula above the level of the centre of the optic disc, and facing one of these is a large coloured plate of the fundus with the macula in its normal position below this level.

In the twentieth edition of Gray's *Anatomy, Descriptive and Applied* the optic nerve is said to enter the eyeball "3 mm. to the nasal side and a little below the level of the posterior pole"; while, in the picture of the posterior half of the left eye, the optic disc is shown in its correct position above the level of the macula.

Similar descriptions to those found in Gray's *Anatomy* occur in the fourth edition of Cunningham's *Text Book of Anatomy.* In a curiously worded passage, after stating that the macula lutea is at the posterior pole of the eye, the optic disc is said to be on a lower level than the posterior pole; and some pages later this statement is repeated. But in a picture of the fundus the optic disc is seen on a higher level than the macula.

In the fifth edition of his *Manual of Practical Anatomy* Cunningham states that the optic nerve enters the eye 3 mm. to the nasal side of, and 1 mm. below, the posterior pole; and Testut's figure is reproduced showing the entrance of the optic nerve into the eye, as seen from behind, with the nerve below the horizontal meridian.

A. M. Buchanan, in his *Manual of Anatomy*, states in three places that the optic nerve entrance is below the level of the posterior pole.

Two passages in *The Anatomy of the Human Eye* by Arthur Thomson clearly state that the point of entrance of the optic nerve is below the level of the posterior pole of the eye.

Similar statements relating to the relative positions of the optic nerve and posterior pole, together with misleading pictures, occur in the works on Human Anatomy of George A. Piersol and of Spalteholz, in Maximilian Salzmann's work on the Anatomy of the Eye, and in the Surgical Anatomy of C. R. Whittaker.

In *A Treatise of Human Anatomy* by H. Morris, the article on the Eye was written by R. Marcus Gunn, at that time Senior Surgeon at Moorfield's Eye Hospital. Here there is no mention of the optic disc being below the level

of the posterior pole, and no picture giving a wrong impression as to the relative positions of the optic disc and the macula. The statement made by Testut that the macula is at the posterior pole is found here also—"at the posterior pole of the eye a small spot (fovea centralis) exists."

Improper statements in works on Human Anatomy as to the relative positions of the macula lutea and the optic disc are inexcusable—the ophthalmoscope will reveal in a moment the truth to anyone who cares to verify his statements. Inconsistencies between the figures and the text are equally reprehensible.

Conflicting statements regarding the posterior pole of the eye can however be readily explained, for there is more than one possible axis of the eye.

In most, if not all, of the works on Anatomy already referred to there is evidence of confusion of thought in this matter. A notable example of this occurs in Buchanan's *Manual of Anatomy* (1914). On page 1383 we find "The centre of the corneal segment is called the anterior pole, and the centre of the sclerotic segment is known as the posterior pole. The sagittal (antero-posterior) axis, or axis of vision, of the eyeball is represented by a line connecting the anterior and posterior poles." On page 1384, "Posteriorly the eyeball receives the optic nerve, which pierces the sclerotic coat at a point about $\frac{1}{8}$ inch to the inner side of, and about $\frac{1}{24}$ inch below, the posterior pole."

Again on page 1384, "It (the optic entrance) is situated, as stated, at a point about $\frac{1}{8}$ inch to the inner side of, and about $\frac{1}{24}$ inch below, the posterior pole of the eyeball." On page 1395, "The internal surface presents in the line of the visual axis of the eyeball, the macula lutea or yellow spot, where vision is most distinct."

The last statement is a perfectly true one, if by visual axis is meant the line of vision, which is, however, by no means the same thing as the axis of vision defined on page 1383. On the other hand if "visual axis" and the "axis of vision" on page 1383 are the same axis then the posterior pole is at the yellow spot, and all the statements about the optic disc being below the posterior pole are manifestly false.

There appears to be a general agreement amongst anatomists to describe an anterior pole of the eye as being the centre of the front of the cornea, a posterior pole as being the centre of the posterior curvature, and the line joining the poles the sagittal axis.

Testut's definition of the poles is more cautious. He says: "Les pôles sont les deux points de la surface extérieure de l'œil que traverse le diamètre antéro-postérieur de cet organe: le pôle antérieur correspond au centre de la cornée transparente; le pôle postérieur est situé au point diamétralement opposé, un peu en dehors de l'orifice d'entrée du nerf optique." Elsewhere Testut is definitely committed to the statement that the macula is exactly at the posterior pole.

Maximilian Salzmann is more cautious still. He says that the midpoint of the cornea forms the anterior pole of the eyeball, and that diametrically

opposite this is the posterior pole "in der nicht weiter anatomisch charakterisiert ist, also nur durch Konstruktion oder Messung gefunden werden kann. Die Verbindungslinie beider Pole ist die geometrische Achse des Augapfels." He points out that an optic axis, in the strict mathematical sense, only exists very rarely—the foci of the three principal refracting surfaces generally lying on a line which is by no means a straight one. He then goes on to state that the line of sight is very different from the geometrical axis, for the fovea, he says, lies to the temporal side of and below the posterior pole. Later on he says that the midpoint of the head of the optic nerve is about 3 mm. to the nasal side of, and 1 mm. below, the posterior pole. Unfortunately no details of measurements of so and so many normal human eyes are given either by Testut or Salzmann to convince one that Testut is right in stating that the yellow spot is exactly at the posterior pole of the sagittal axis, or that Salzmann is right in saying that the fovea is below the posterior pole. I have not been able to find any anatomist who quotes his authority for stating that the optic disc and macula bear such and such a relation to the posterior pole of the eye.

Doubt as to the propriety of stating that the macula is situated at the posterior pole has evidently arisen in the mind of the author of the article on the Eye in Gray's *Anatomy, Descriptive and Applied.* In the eighteenth edition (1913) we read: "Exactly in the centre of the posterior part of the retina...is...the macula lutea." In the twentieth edition (1918) this has become "Near the centre of the posterior part of the retina is...the macula lutea."

It seems to me most probable that anatomists have in their minds the researches of Helmholtz and Tscherning on the optic axis. These observers showed that the optic axis (i.e. the line passing through the nodal point and the centre of rotation of the eyeball) cuts the region of the posterior pole on the inner side of the yellow spot and slightly above it. But the optic axis is, by definition, a different axis from the anatomical sagittal axis, and the confusion of one with the other is certain to lead to wrong descriptions. Moreover this statement of Helmholtz, confirmed by Tscherning, does not mean that the optic disc is below the level of the posterior pole, for the optic disc is itself slightly above the level of the macula.

Would it not be wise to avoid this morass of conflicting statements by not using the posterior pole as an anatomical landmark, when it has no characteristics of a landmark? It would be simpler and more accurate to make the yellow spot the central landmark for this region, and state the plain truth that it is situated in the region of the posterior pole of the eyeball.

The centre of the optic disc will usually be found to be at about the level of the upper edge of the macula. Often the optic disc occupies a still higher position, more rarely the centre of the disc and centre of macula are on the same level. I have only once seen the centre of the disc below the level of the macula. It is certainly an exceedingly rare position.

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THE MICROSCOPICAL STRUCTURE OF THE ENAMEL OF TWO SPARASSODONTS, CLADOSICTIS AND PHARSOPHORUS, AS EVIDENCE OF THEIR MARSUPIAL CHARACTER: TOGETHER WITH A NOTE ON THE VALUE OF THE PATTERN OF THE ENAMEL AS A TEST OF AFFINITY

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THE question of the existence of any relationship between the Creodonts and modern carnivorous Marsupials is one which, owing to the close resemblance in their dentitions, has attracted much attention from palaeontologists. The form and pattern of teeth afford valuable data in establishing such relationships, but closely similar dentitions may be evolved in creatures of widely divergent ancestry as in the case of the Dog and the Thylacine. Consequently, any essential character which enables an investigator to state definitely from the examination of a fragment of a tooth, as to the precise relationship of its possessor, is of great value.

Such a character exists in the structure of the enamel of the teeth of Marsupials. The late Sir John Tomes in a classical paper (1) demonstrated the fact that with one exception—the Wombat—all recent Marsupials possess enamel on their teeth characterized by the presence of tubes continuous with the dentinal tubes. These enamel tubes are occupied by an organic fibril, the tube being merely the channel in which the fibril lies surrounded by the enamel without the intervention of an intermediate substance.

In 1906, Sir Charles S. Tomes published a paper entitled "On the Minute Structure of the Teeth of Creodonts, with especial reference to the suggested resemblance to Marsupials" (2), in which he employed this distinctive character, first demonstrated by his father, in the endeavour to find whether the structure of the enamel in these fossil forms disclosed any evidence as to their Didelphian or Monodelphian affinities, but states that "in the interpretation of the occurrence of this character a different value appears to attach to negative and positive results: if we find no tubes at all in the enamel we shall, I think, be quite justified in saying that no near affinity with the Marsupials can exist. On the other hand, if we find rudimentary traces of this penetration, we shall not be justified in attaching great importance to it as an evidence of Marsupial affinity, though if we find an abundant penetration we shall have a character which, so far as is known, is peculiar to Marsupials and to Hyrax."

Tomes prepared sections from teeth of Hyaenodon, Mesonyx, Pachyoena, Oxyoena, Sinopa, Didymictis, Cynodictis and Borhyoena.

The explorations of Ameghino have led to the discovery in Patagonia of a number of forms—Cladosictis, Procladosictis, Pseudocladosictis, Amphiproviverra, Perathereutes, Acyon, Prothylacinus, Borhyoena, Pseudoborhyoena, etc. from the Santa Cruz and Casa Mayor formations, and Proborhyoena and Pharsophorus from the Deseado formation—which exhibit in a large number of characters a most marked resemblance to existing polyprotodont Marsupials.

Scott (3) writes: "The differences are of three kinds: (1) there are no vacuities in the bony palate; (2) the milk dentition is less reduced, the canines and one or two premolars being changed; (3) the enamel of the teeth in the only genus (Borhyoena) which has been examined microscopically, resembles in its minute features that of the placentals and lacks the Marsupial characters.

Though by no means unimportant, these differences are altogether outweighed by the thoroughly marsupial nature of all other parts of the skeleton, and I cannot but agree with Dr Sinclair in including them with the Tasmanian Thylacine."

Dr Sinclair's memoir (4) constitutes the most authoritative and exhaustive account yet published dealing with these fossil Thylacinidae, in which family he placed most of the forms included by Ameghino in his sub-order, Sparassodonta. He writes: "In connection with the question of the descent of the Patagonian and Tasmanian Thylacines from a common ancestor it may be interesting to notice that certain large Carnivorous Marsupials from the Pyrotherium beds (Ameghino, 1897) named by Ameghino, Proborhyoena and Pharsophorus retain the metaconid in the lower molars whilst the premolar formula is unreduced. The loss of the metaconid in the Thylacinidae separates them sharply from all other carnivorous marsupials. It is possible that these two genera mentioned, in which this cusp is retained, will be found to occupy an intermediate position between the Thylacinidae and Dasyuridae, but until they are better known it is unsafe to attempt generalizations of so broad a character."

As Scott mentions, the enamel of one only of these extinct Thylacinidae has been examined: this was done by Tomes who prepared sections from a fragment of a tooth of Borhyoena, now regarded as a Sparassodont, but included by him amongst the Creodonts. His description states "Borhyoena. In this genus we find the absence of penetrating tubes and *we can distinctly recognize the carnivorous pattern in the course of the prisms.* But apparently the prisms are a little straighter than in recent Carnivora, or at least in recent Felidae. It is not, however, possible to speak very positively as to their greater simplicity, as I had only a fragment of a tooth at my disposal, and the sections I was able to get were small, and may not have included any of the thickest parts of the enamel where, as has already been noted, these characters are to be found most marked. *However, there is ample evidence to say that the enamel of Borhyoena is essentially of the Carnivorous type and bears no more resemblance to Marsupials than does that of other Creodonts.*" (The italics are mine.)

The conclusions of Tomes, though negative, in so far as he found no evidence

of "penetration" of the enamel by tubes, have been of considerable weight with palaeontologists in their estimation of relationship of the Creodonts and of the Sparassodonts, but the evidence of the Marsupial affinities of the Patagonian forms is so overwhelming that Mr D. M. S. Watson, Lecturer in Vertebrate Palaeontology at University College, suggested that I should examine the enamel of Pharsophorus (from the Deseado formation of Patagonia, Oligocene).

Dr C. W. Andrews, F.R.S. (British Museum, Natural History) very kindly gave me one of the cheek teeth from which I have been able to prepare a number of sections. All of these preparations disclose the typical Marsupial character of the presence of "tubes" (*t*) in the enamel (*e*). It will be seen (Plate XX, fig. 1) that the enamel prisms leave the dentine surface at an angle of about 45° and pursuing an almost straight course, run outwards until but a short distance from the free surface where there is a slight change of direction.

Mr Watson also obtained for me from the American Museum of Natural History, through the generosity of Dr Matthew, a portion of the crown of a cheek tooth of Cladosictis (from the Santa Cruz formation of Patagonia, Miocene) from which I have prepared several sections. In each of these also the characteristic Marsupial structure of the enamel obtains (Plate XX, fig. 1).

The enamel in my sections of the tooth of Cladosictis is peculiarly refractile making it difficult to obtain a clear photomicrograph showing the direction of the enamel prisms but the course which they pursue is somewhat similar to that seen in illustration of the enamel of Pharsophorus (Plate XX, fig. 1). The tubes of the enamel in these sections are very markedly spiral in their course and, by careful focussing, can be followed through most of the thickness of the enamel, but naturally this does not show very clearly in a photomicrograph which reproduces but one plane.

I have had no opportunity of examining the enamel of Borhyoena (fragments are scarce and but two complete skulls have been found) but its affinities are so close to the specimens examined that I have little doubt that, with a sufficiency of material, the presence of tubes in the enamel will be demonstrated[1].

As C. S. Tomes states: "The examination of fossil teeth presents greater difficulties than those of recent teeth. Structurally the enamel is always well-preserved, but it has in the process of mineralization, often become unduly transparent, so that careful illumination is even more essential in deciphering its structure. And the teeth are often exceedingly brittle and friable, so that it is difficult to get good sections....The dentine, however, being richest in organic

[1] Since this paper has been in the hands of the printers I have received a considerable portion of the crown of a cheek tooth of Borhyoena from which I have prepared twelve sections of the enamel with the adjacent dentine. These sections range from the tip of the cusp to the neck of the tooth and in all there is penetration of the enamel by "tubes" which in some cases pass from the dentine through the greater thickness of the enamel.

Over the apex of the cusp the pattern of the enamel is somewhat complex, the prisms running in groups or sheaves, but in all other parts of the crown of the tooth their course is almost straight, passing out from the dentinal surface at an angle of about 60°. (1. v. 1920.)

matter, is often very badly preserved so that sometimes all structure has disappeared: a fact which handicaps the observer in tracing the passage of tubes from it, and sometimes leaves him only able to look for characteristic appearances of tubes in the enamel itself. Moreover, many of the teeth being rare, only small bits of damaged teeth were available for examination, so that it was not always possible to select the plane in which a section was most desirable: one had to take what one could get."

In the examination of a considerable number of fossilized teeth I have encountered the same obstacles as did Tomes and have learned to appreciate the difficulties which exist in arriving at a definite conclusion as to the presence or absence of certain characters. One fortunate section may disclose these characters, but when negative results only are obtained, the one safe course seems to be to withhold an opinion until an abundance of material is available.

In his examination of the teeth of Creodonts, Sir Charles Tomes employed in addition to the Marsupial character of "penetration" of tubes, another criterion in the general pattern assumed by the enamel prisms. He writes: "A general character of marsupial enamels is the simplicity of the course pursued by the enamel prisms, each prism pursues as a rule an almost straight course from the dentine to the enamel surface, and where marked curvatures do occur, all of the contiguous prisms pursue the same course so that no patterns are produced by neighbouring prisms crossing one another. Where, however, the tubes are very abundant, the enamel prisms can hardly be seen at all, and we have to take the tubes as indicative of their course."

Of Carnivora, he writes: "...The enamel patterns of Carnivora are fairly constant. As one would expect from analogy, they are not quite identical in all: thus in the Dog group they are simpler, and where the enamel is thin they become quite straight. Where, however, the enamel is thicker, the patterns are easily identifiable as similar to those found in, for example, the Felidae, though the curvatures are less pronounced...."

In Hyaena "It will be noticed that no prisms in this, the thicker portion of the enamel, pursue a straight course and that all do not pursue the same course. *They are, however, grouped into bundles or sheaves of prisms pursuing an approximately parallel course, whilst towards the exterior of the enamel all the bundles become parallel and straight. They are thus interwoven with one another in a way that is not found in any known Marsupial.*" (The italics are mine.)

Taken in conjunction with other anatomical characters, I regard the presence of tubes in the enamel as a precise test of Marsupial affinity, but I think too much importance must not be attached to the pattern of the enamel in determining affinity between members of different orders, however useful such a test may be when applied to members of the same order, for I agree that in the case of most recent Carnivora, in those areas where the enamel is thick, a general sort of pattern is produced by the interweaving of groups of prisms.

In Cynodictis, however, which is not a Creodont but one of the Fissipedia and therefore a true Carnivore, Tomes found that "the enamel prisms are

almost straight and no decussation, or only the faintest trace of decussation of the prisms of different planes is to be seen. It resembles chiefly the enamel of Didymictis and differs in respect of its greater simplicity from that of other Creodonts examined and from recent Carnivora. My sections of Cynodictis embrace the whole tooth, so that there is no question as to the greater complexity of pattern existing in any other part of the tooth."

Of Didymictis, one of the Miacidae, of the Palaeocene and lower Eocene, a Creodont family ancestral to the Fissipedia, but so highly specialized in its Carnivore characters that Scott (*op. cit.* p. 557) is of opinion it should be regarded as a true Carnivore, Tomes writes: "the enamel prisms are parallel and pursue a course only slightly curved. The typical carnivorous pattern is not to be found, nor is there any trace of it, so that of the Creodonts examined this and Cynodictis stand alone in this respect."

Here then we find that in an early true Carnivore and in a form ancestral to it the typical pattern which Tomes regards as characteristic of Carnivore enamel is absent.

In Borhyoena, now regarded by Sinclair, Scott, Andrews and others as an undoubted and highly specialized predaceous, polyprotodont Marsupial, Tomes in his sections distinctly recognizes "the carnivorous pattern in the course of the prisms....However there is ample evidence to say that the enamel of Borhyoena is essentially of the Carnivorous type and bears no more resemblance to that of Marsupials than does that of other Creodonts."

In connection with other investigations I have examined a large number of teeth of representatives of most genera of Marsupials: in some cases a head has been taken and sections prepared from every tooth for the purpose of comparing the structure obtaining in different members of the same dental series, and I may state that the pattern of the enamel in recent Marsupials is not so simple as the description given by Tomes, and quoted earlier in this paper, would lead us to suppose.

In Plate XXI, fig. 1, is reproduced a photomicrograph from a section of the enamel of Dasyurus where the prisms are seen to be "grouped into bundles or sheaves of prisms pursuing an approximately parallel course...interwoven with one another in a way" which Tomes states "is not found in any known Marsupial."

A photomicrograph taken from a section of the apex of one of the cheek-teeth of Macropus ruficollis is reproduced in Plate XXI, fig. 2, where it is seen that, contrary to Tomes's assertion, the prisms in Marsupial enamel may cross one another, producing a pattern.

Tomes also states that "when the [enamel] tubes are very abundant the enamel prisms can hardly be seen at all and we have to take the tubes as indicative of their course." From his investigations on the development of Marsupial enamel (5) he arrived at the conclusion that the tubes lie in the axes of the prisms, his view being that in development each enamel cell is furnished with a prolongation of its cytoplasm which extends through the whole thickness of the forming enamel, and that calcification proceeds centripetally in these

processes, in some cases leading to a complete obliteration with a resulting solid prism, whilst in others calcification does not proceed so far and the resultant uncalcified prolongation of the enamel cell constitutes the "tube" which, therefore, is confined within the limits of one prism.

Were this view of development correct the tubes would be indicative of the course of the prisms: but the difficulties encountered in interpreting the structure of enamel are made evident when it is found that eminent authorities differ in their views as to the position occupied by the tubes in the enamel. As stated above, Tomes considers them to lie within the prisms whilst Mummery (6) is convinced that they invariably lie in the interprismatic material, his view being that spaces exist between the prisms of the forming enamel and that the dentinal fibrils insert themselves into these areas.

Tomes states ((7), pp. 51, 52) that von Ebner considered that "the tubes in Marsupial enamel do not lie in the rods themselves but in their interspaces, and he gives a figure of a transverse section in which all but one of the tubes appear to do so. Leon Williams has photographed some transverse sections of marsupial enamel in which three-fourths of the tubes appear clearly to be in the substance of the rods. The remaining fourth appear as though they were between them."

I have a number of preparations, some of which have been reduced to a thickness of 5μ, which agree with the appearances seen in Leon Williams's photographs.

Reference to Plate XXI, fig. 3, will, I think, demonstrate clearly that the course of the enamel tubes and their occupying fibrils is not associated with or dependent upon the direction of the prisms; they may proceed parallel with the prisms, lying in the interprismatic area: or they may lie within the substance of the prisms: or they may proceed at right angles to or tangentially across groups of prisms.

The facts stated above and demonstrated in the illustrations figured in Plate XXI, lead me to attach restricted value to the pattern of the enamel as a determining character in deciding affinity.

I have been able to examine the enamel of one Creodont only, the highly specialized Hyaenodon, for which tooth I am indebted also to Dr Andrews, but the sections obtained from this lead me to think that a re-examination of the microscopic structure of enamel in the more primitive Creodonts, should be undertaken.

In Hyaenodon Tomes "found no trace of penetration by tubes" but my sections do disclose such a penetration as may be clearly seen in Plate XXII, figs. 1 and 2 (*t*), where the tubes, though infrequent, extend some distance into the enamel.

The general pattern of the enamel is shown in Plate XXII, fig. 3, which is from a photomicrograph of a section which had been etched to bring out the pattern.

So it is seen that in a Creodont this pattern which Tomes regards as characteristic of Carnivora can exist together with that peculiarly Marsupial character of the "penetration" of the enamel by tubes.

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Fig. 1.

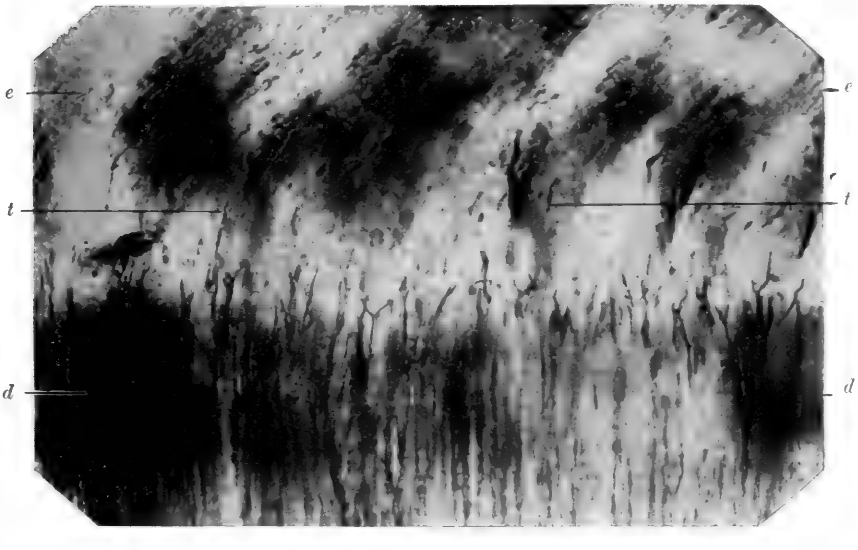

Fig. 2.

Fig. 1.

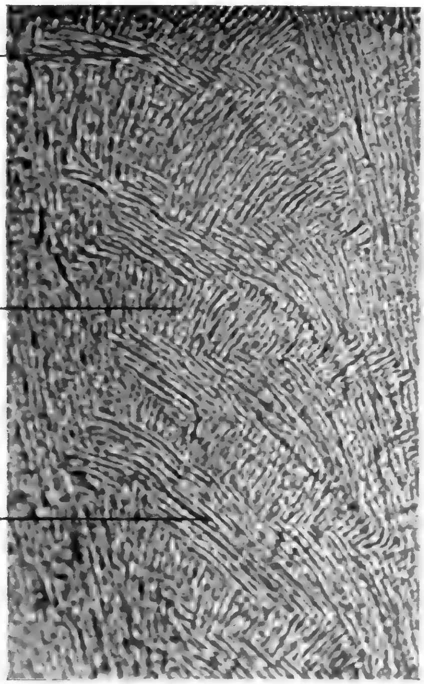

Fig. 2.

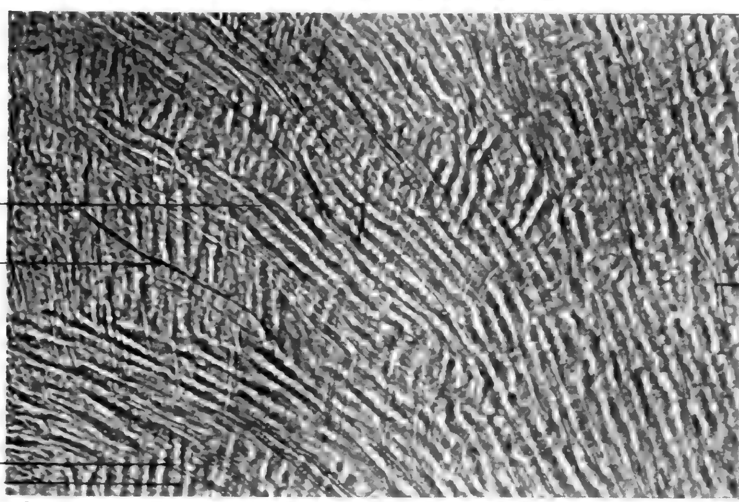

Fig. 3.

The result of this investigation is to demonstrate that the two genera of Sparassodonts examined possessed typical marsupial enamel and thus the points of difference in the skeletal characters between these extinct Thylacinidae and recent carnivorous marsupials become reduced to two only.

Further, the demonstration of the fact that recent marsupials may, in the structure of their enamel, disclose patterns which have been regarded as essentially typical of Carnivora, and that Hyaenodon possessed enamel which exhibits a "penetration" by tubes, may be regarded as additional evidence in favour of the common origin of the Marsupials and the early Monodelphia. In the ultimate solution of this problem the evidence afforded by the minute structure of the teeth may prove a deciding factor.

In conclusion I desire to express my thanks to Mr D. M. S. Watson for asking me to undertake this work; to Dr C. W. Andrews, F.R.S., and to Dr Matthew for entrusting me with such rare and valuable material: and to Mr F. J. Pittock, of the Zoological Department of University College, for taking the beautiful microphotographs reproduced in the illustrations.

To Professor J. P. Hill, F.R.S., I owe a constant and increasing debt of gratitude for affording me facilities to carry on research under his inspiring direction and with the invaluable advantage of his advice and criticism.

DESCRIPTION OF PLATES

Reference Letters

d. dentine; *e.* enamel; *p.* prism; *t.* tube.

Plate XX

Fig. 1. *Cladosictis.* Section of a tooth showing the penetration of the enamel (*e*) by tubes (*t*) continuous with the dentinal tubes (*dt*). Microphotograph × 320.

Fig. 2. *Pharsophorus.* Section of a cheek tooth presenting the tubes in the enamel (*e*) continuous with the dentinal tubes. Microphotograph × 360.

Plate XXI

Fig. 1. *Dasyurus.* Section of enamel from a cheek tooth showing the prisms arranged in bundles. Section etched to bring out the pattern. Microphotograph × 280.

Fig. 2. *Macropus ruficollis.* Section of apex of a molar tooth showing the pattern produced by the crossing of groups of prisms. Etched. Microphotograph × 160.

Fig. 3. *Macropus.* Section of enamel, etched with acid, showing that the tubes (*t*) do not necessarily follow the direction of the prisms (*p*). Microphotograph × 320.

Plate XXII

Figs. 1 and 2. *Hyaenodon.* Sections of a tooth showing the presence of tubes in the enamel. Microphotograph × 360.

Fig. 3. *Hyaenodon.* Section of tooth which has been etched to bring out the pattern of the arrangement of the enamel prisms. Microphotograph × 120.

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A CYCLOPS LAMB (*C. RHINOCEPHALUS*)

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The occurrence of one-eyed monsters has excited the wonder and curiosity not only of the men of our own period but also of the ancients. Among the latter Homer stands out pre-eminently, and his tale of the adventures of Ulysses, and his fellow-travellers, with the giant Polyphemus, has fascinated and stimulated the imagination of all students of mythology.

The questions which these ancient lays suggest, are:

1. Is there any foundation in fact, for the classical myths of a race of giant cyclopes living apart from the world in insular seclusion?

2. Is it possible for human cyclopes to reach maturity and have normal vision?

It seems probable that the idea of a race of one-eyed monsters has arisen from the occasional birth of such among animals and men; and that the myths which have grown out of this idea have gradually evolved in the imaginations of the poets and historians of the past, rather than that they have been evolved, as it is alleged by some, upon a basis of allegorical construction; or that they are explainable on the assumption that there were races who fought with helmets, constructed with a single opening in front, which gave rise to the appearance of a single eye.

Among the records of mammalian cyclopean monsters we have not found any mention of such having survived their birth by more than a few hours or days[1].

From a cursory examination of published cases, the explanation of the early death of these monsters appears to be due to the difficulty which is experienced by the young in suckling. In those cases in which the cyclopic defect is combined with a high degree of "agnathia" (10), this would of course be impossible, owing to the pharynx ending blindly, and having no communication with the mouth or nasal cavities. The young would thus quickly die from suffocation. But there are a large number of cases such as the specimen which forms the subject of this paper in which the mouth cavity communicates freely with the pharynx. In the majority of these cases, however, the nasal cavities are completely shut off from the pharynx (fig. 4), which ends in a blind recess at the base of the skull. The young would thus be

[1] Regnault has figured a case of a cyclocephalic foal which was said to have lived for about 4 months. Geoffroy Saint-Hilaire however, who quotes the case, believes that the history is not authentic, and that the case ought not be taken into consideration.

prevented from breathing during the act of suction, and the process of suckling would have to be carried out by alternate respiratory and suction movements. Under these circumstances it is not surprising that the vast majority if not all cases of cyclopia occurring in mammals should not survive their birth by more than a few days.

It has been shown by Geoffroy St Hilaire (23), however, that cyclops monsters, whether human or occurring in domesticated animals, such as the sheep, horse, pig, dog or cat, do not survive their birth by more than a few hours, some being described as dying suddenly in convulsions in less than twenty minutes after birth. This he attributes to the same cause as that which results in the very early death of the *anencephalia*, namely a grave defect in the development of the brain. It is, therefore, only in the lesser degrees of deformity which are unaccompanied by defect in the growth of the brain, and in which both the mouth and nasal cavities communicate with the pharynx that it would be possible for the individual to survive. In fact not the true cyclopes in which there is a single median eye, but those cases in which there is merely an approximation of the eyeballs, without any marked defect in the development of the nasal chambers.

With regard to the possibility of a cyclope possessing normal vision, we find that in nearly all the published cases in which a dissection has been made of a median eye, that the interior of the eyeball is almost completely filled with choroid, and no mention is made of either retina or vitreous. Moreover, the lens has been found double, or if single, it has usually shown indications of its composite nature. It is extremely improbable, therefore, that if it were possible for a human cyclope to reach maturity, he would possess normal vision.

The specimen of cyclops lamb (figs. 1 and 2) which forms the subject of this paper, belongs to the class described by Geoffroy St Hilaire, as *C. Rhinocephalus*. The name indicates the presence in this variety of a trunk-like appendage, or proboscis. This contains the rudiments of the olfactory portions of the nasal chambers, and projects upward from the frontal region above a single orbital cavity.

Viewed from in front fig. 1, there may be noted (1) the proboscis (3·5 cm. in length) turned upwards and backwards over the frontal region. Its external opening shows an indication of bilateral subdivision into right and left nostrils. At its base a pointed process of bone somewhat triangular in form could be felt projecting upwards from the centre of the supraorbital margin. In the subsequent dissection of the head, this proved to be the premaxillae fused one with the other and displaced upwards above the eyeball. Below the proboscis is (2) the composite median eye, which occupies a rhombic area corresponding to the fused right and left palpebral apertures. The lateral angles of this area are formed by the external canthi. The right and left upper eyelids are continuous with one another at the superior angle, and the lower lids unite at the inferior angle. In the middle is a vertical

Fig. 1. *C. Rhinocephalus*, viewed from in front.

Fig. 2. *C. Rhinocephalus*, viewed from the side.

fold of conjunctiva which represents the fused "plicae semilunares," and which lies between two corneae. These are situated one on each side in the anterior wall of a single median eye, the transverse diameter of which considerably exceeds the vertical. Below the orbit is (3) a short upper lip, and projecting beyond this (4) the tip of the tongue, which is turned upwards towards the eye. Below this again is (5) the lower lip, which projects forward (see fig. 2) a short distance beyond the upper lip.

On making a dissection of the bones of the skull (fig. 3), it was seen that the root of the proboscis is supported on its under part by the premaxillae which are united with each other in the middle line, and displaced upward. Their basal or palatine parts together form the median part of the roof of the common orbital cavity. Laterally they are connected by fibrous tissue to the frontal and nasal bones. Dorsally the root of the proboscis is formed by the two nasal bones, which are very much shortened. Behind they

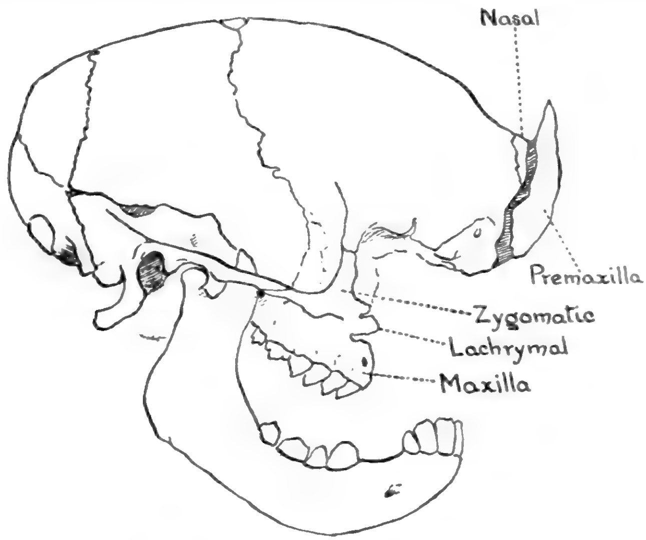

Fig. 3. Lateral view of skull.

articulate with the frontal bone, while anteriorly they are united with the premaxillae by membrane. The single orbital cavity is wider in the transverse diameter, than a normal right or left orbit. This is owing to the participation of the outer and middle parts of both orbits in the formation of a single large median cavity. The median walls of the orbits formed usually by the sphenoid, ethmoid and lachrymal bones are absent. The lachrymal bones having been displaced downwards, form part of the floor of the orbital cavity, and the central part of the infra-orbital margin; while the ethmoid is displaced upward, and forms part of the skeletal basis of the "proboscis."

The orbital margin is formed above by the basal or palatine parts of the premaxillae, and supra-orbital margins of the frontal bones; laterally by the

external angular processes of the frontal and the malar bones; below by the infra-orbital processes of the malar bones, and the two lachrymals. The single optic foramen is continuous on each side with the superior orbital or sphenoidal fissure.

The upper jaw is markedly shortened and is composed of the alveolar portions of the maxillae only; the premaxillae taking no part whatever in its formation. In it are contained the normal number of teeth, viz.: three premolar and three molar.

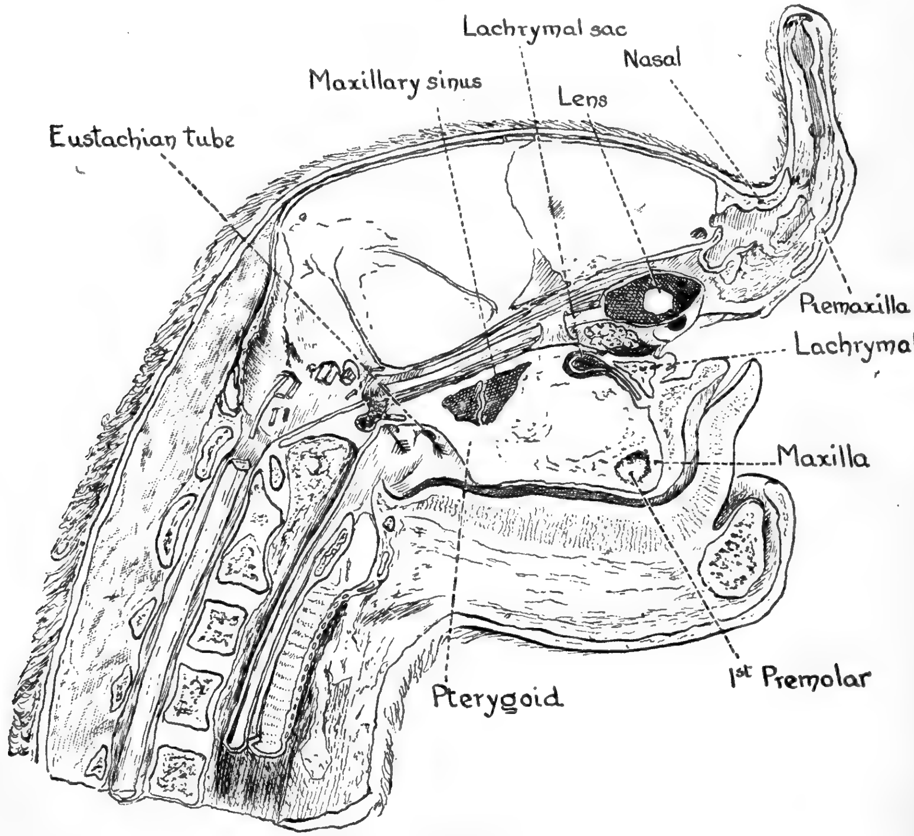

Fig. 4. Median section of head.

The anterior part of the lower jaw, which is unopposed by the premaxillae is curved upward. In it one can recognise three incisor, and one canine, anteriorly, and the normal number of premolar and molar teeth behind.

The remaining parts of the skull as viewed from the lateral aspect appear normal.

On making a longitudinal section of the head and neck (fig. 4), the cavity of the proboscis was seen to lead down from the single 8-shaped opening formed by the right and left nostrils into a large tubular space which extended to the root of the proboscis. Here the inner membrane appeared to be continuous

on each side of the crista ethmoidalis with the dura mater of the anterior fossae of the skull. The interior of the proboscis was partially subdivided into right and left nasal cavities by an irregular septum formed by rudiments of the mesethmoid and vomer. Laterally there were some nodular projections representing the ethmoturbinals. The apparent openings in the region of the cribriform plate leading from the cranial cavity into the trunk were occupied by three flask-shaped evaginations of the dura mater. These were connected by nerve fibres with the olfactory lobes.

Below the anterior cranial fossae the section passed through the orbital cavity in the middle of which was the single eyeball. The cavity of this was almost completely filled by choroid, but contained in addition two lenses, of which the right was the larger. In correspondence with these there were two anterior chambers, the iris and the cornea of the right side being larger than on the left. On the floor of the orbit were the two lachrymal sacs; that on the left side was prolonged downwards and forwards into a narrow tube which ended blindly; on the right side the duct was complete, and opened into the lower part of the right nasal cavity, beneath an overhanging ridge which appeared to be the maxilloturbinal. It was evident therefore that the nasal chambers were divided into two parts; an upper or olfactory part lying above the orbit, and contained within the proboscis, and a lower maxillary part, represented on the right side only, and closed both in front and behind. In the remaining part of this region the saw had passed through bone; the section having traversed parts of the fused maxillae, lachrymal, palate and pterygoid bones. Anteriorly by breaking away the bone overlying it, an alveolus containing the first left premolar tooth was exposed; and by a similar method the cavity of the left maxillary air sinus was opened up. The nasal region was limited behind by a well defined sloping border which was formed by the posterior margins of the fused internal pterygoids. This constituted the anterior boundary of the naso-pharynx, which was thus entirely cut off from the nasal cavities. The lateral walls of the naso-pharynx were closely approximated, its transverse diameter thus being greatly lessened. The lower orifice of the Eustachian tube and a pharyngeal recess were visible on each side. The pharynx was continuous with the buccal cavity through a slit-like opening bounded laterally by the anterior pillars of the fauces. The anterior part of the roof of the mouth was absent, the premaxillary portion having been displaced upwards above the orbit. The upper lip appeared to be formed by the labial portions of the embryonic maxillary processes only, the central portion which is normally formed from the medial nasal processes being displaced upward from this region into the proboscis. The roof of the mouth was thus considerably shortened, and the tongue which protruded beyond the upper lip was bent sharply upward towards the eye.

A median longitudinal section through the brain, showed that the cavity of the third ventricle was almost completely obliterated, by fusion of the optic thalami, and that there was a complete absence of the corpus callosum.

A single optic nerve passed forwards from the optic chiasma to the posterior pole of the eyeball. The remaining cranial nerves were seen to occupy their normal situations with the exception of the **IV** nerve which appeared to be absent.

On removing the roof of the orbit, we were able to recognise the right and left *levator palpebrae superiores* muscles, lying superficially on each side of the median plane, and fused by their medial borders. Beneath were the superior *recti* also fused. The superior oblique, and internal *recti* muscles were absent, and only traces of the inferior oblique and inferior *recti* muscles could be recognised. The lateral *recti* were present, and well developed. Branches of the third nerve, and the sixth nerve supplied the muscles described above, and the supra-orbital and lachrymal branches of the ophthalmic nerve were present.

ETIOLOGY

The cause of "cyclopia," and the frequently associated defect "agnathia" has been investigated by many authors and experimental embryologists, more especially Meckel (17), Geoffroy St Hilaire (23), Huschke, Dareste (5), Born, Spemann (25), Driesch (6), Fischel (7), Stockard (26) and E. Schwalbe (24), and a considerable number of theories have been advanced in explanation of the condition. The more important of these have been summarised by Ernst Schwalbe in his work entitled, *Die Morphologie der Missbildungen des Menschen, und der Tiere*, Teil III. It will therefore be unnecessary to do more than record certain conclusions, which we have come to, from a study of the specimens which we have examined.

In the description of a specimen of a cyclops and agnathic lamb published by one of us in 1910 (10), it was pointed out that a distinction may be drawn between those cases of cyclopia which occur in double- and those which occur in single-monsters. As a type of the former, which illustrates the condition best, we may select the well-known class cephalothoracopagus disymmetros.

In these monsters there is a composite head which has the appearance of having been formed by the fusion face to face of the heads of two separate embryos with one another; there being two completely separated bodies, having their ventral aspects opposed, and each bearing the normal complement of upper and lower limbs. The condition, however, as has been shown by E. Schwalbe, appears to be due not to fusion of two embryos, but to an extensive posterior dichotomy of a single embryo. In the dichotomy everything but the most anterior part of the cephalic end of the medullary plate is involved. The two partially separated heads have grown in contact with one another, so as to produce a large double-head, on the opposite sides of which are two composite faces. The right and left halves of each face are formed from the opposed halves of each head. As the longitudinal axes of each head are seldom in line with one another, but join at an angle, one face is often more completely developed than the other, namely the one corresponding to the side on which the axes would unite so as to form a projecting angle,

whereas on the opposite side corresponding to the receding angle, the composite face is imperfectly developed, the lateral parts of the face being approximated and the central parts defective or absent. On this side a single composite eye, and external auditory meatus may be present, and the nose and mouth rudimentary or absent. Here the growth of the two partially separated heads has been interfered with by contact of one head with the other; thus, the mouth and nose, and the nasal halves of the eyeballs remain undeveloped, whereas the outer parts of the two faces are free to grow. The single eye is thus formed by the temporal halves of the right and left eyes belonging respectively to the right and left foetuses grown forward in continuity with one another, the nasal halves being suppressed; not by a right or left eye belonging to a single head, as might occur if an irregular fusion had taken place between the heads of two separate individuals.

The formation of the single composite eye in these monsters furnishes we believe an explanation of the mode of development of cases of cyclopia occurring in single-monsters, namely, a defect in that part of the medullary plate from which the floor of the third ventricle and adjoining parts of the lamina terminalis and optic vesicles are developed, and involving also the overlying surface ectoderm and mesoderm. This would allow the temporal halves of the optic vesicles, to grow forward in continuity with one another so as to form a single composite eye, and it would prevent the normal union of the fronto-nasal process, with the maxillary processes. The degree of the deformity will naturally vary with the extent of the primary defect in development; and the parts which are affected, will vary with the exact site of the original defect, and also with the stage of development at which the defect in growth takes place.

The cause or causes of this defect in growth of the central parts of the face, which gives rise to the different degrees of cyclopia and allied defects, is a difficult question which we do not propose to deal with in this paper; we may mention however that the mechanical effect exerted by the pressure of the head-fold of the amnion appears to be disproved, as a general cause, by the frequency with which the defect appears in *anamnia*, and by the symmetry of the parts, which is such a marked feature of the *monophthalmia*.

Recent experiments by American investigators on fish and amphibian embryos indicate that the condition arises from some interference with the general nutrition of the growing embryo, which acts more especially on certain parts, at a particular period of development. It was found, for instance by McClendon (18), that a large percentage of *fundulus* embryos were cyclopic, when reared in water in which the carbonic acid content of the water was considerably above that found in normal pond water, and he got the same results with embryos grown in water in which was dissolved varying proportions of magnesium and other salts. The number affected and the degree of the deformity varied with the strength of the solution, and he also found that different effects followed the use of the deleterious salt at different periods

of development. Similar results were obtained by Stockard (26) who, in addition to magnesium salts, employed alcohol, ether, chloroform and chloretone in varying strengths. It may be presumed therefore that certain parts of the embryo in which growth is especially active at a particular stage in development, would be especially susceptible to the action of the poison, and would suffer more than others if the general nutrition were interfered with. If this assumption is correct, the principle involved is applicable to all classes of vertebrate animals, whether the defect in nutrition is produced by a faulty condition of the water in which the embryos of fishes or amphibia are reared; or with reptiles and birds the nutrition of the embryo in incubated eggs is interfered with by varying the condition of the air supplied, e.g. with regard to temperature and degree of moisture. And in the *placentalia* the same cause will act through varying conditions of the maternal blood circulating through the placenta or of the liquor amnia, or, finally, as a result of endometritis, or a diseased condition of the placenta itself, causing impairment in the nutrition of the embryo.

It may be worth while to point out here, that the special action of chemical substances circulating in the blood, at a later stage of development, on the growth of particular parts, such as the long bones, or the nasal and maxillary regions of the face, may be discounted in this connection; e.g. the supposed action of the thyroid and pituitary secretions on these parts in adolescent and adult subjects in certain forms of gigantism and acromegaly. For in the more extreme forms of cyclopia, and in the allied condition of agnathia, it is probable that the defect in development, occurs at a very early stage in development (Schwalbe and Spemann) before either the thyroid or pituitary glands have become recognisable as definite organs; and in the less marked forms of deformity which occur, from a faulty development taking place at a later stage, e.g. "hare lip," these organs though existing as epithelial pouches would, presumably, not yet be functional.

The theory that the defective development of a particular part or organ, may be due to faulty nutrition of the embryo as a whole, rather than to local and mechanical causes, if true, is of great importance as an explanation of the frequent association in a single individual of one defect in development with another; e.g. *spina bifida*, with "*hare lip*" and *cleft palate*. The general condition which would have interfered with the union of the medullary folds or neural laminae, would also have prevented the union of the embryonic medial nasal processes with the maxillary. The theory also serves as an explanation of the frequent occurrence of congenital deformities of varying types in children born at succeeding pregnancies from the same mother. A general cause such as chronic alcoholism, syphilis, or the imperfect elimination of urea from the system may obviously act prejudicially on the general development of the embryo, and with varying states in the health of the mother, more at one period of development than another. It would however also exert a more especially prejudicial action on particular organs during

certain critical stages in their development, e.g. in the development of the nose and mouth, the period at which union of the palatal processes, with one another and with the nasal septum takes place during the eighth week of intra-uterine life.

We thus see that a connection is established between such apparently widely separated types of deformity as cyclopia or agnathia, and bilateral or single facial cleft, cleft palate or hare lip; all of which may be regarded as variations in degree of deformity between the more extreme, and less extreme instances of defective development. The different stages connecting these malformations are well illustrated in the classification of the varying degrees of cyclopia by Bock (1), and in an important article by the Japanese author, Inouye (13), on the development of the premaxilla, and its bearing on the malformations grouped under the term "facial cleft." The different grades in defective development of the lower jaw, leading up to complete agnathia is too large a subject to deal with in this article, and we propose therefore to describe these in a subsequent paper.

Viewed from the practical standpoint, the dependence of these deformities on defective nutrition due to a general or constitutional cause, serves to emphasize the importance of careful constitutional treatment of women during pregnancy, and more especially the early stages, when the more critical phases of development are taking place.

SUMMARY

The study of this specimen, and allied conditions has served, we believe, to establish the following general conclusions:

1. Cyclopia when occurring in mammalia are as a general rule incapable of surviving their birth by more than a few hours or days; this is owing to interference, by associated defects in the development of the mouth, pharynx and nasal cavities, with the acts of respiration or suction, and frequently owing to grave defects in the development of the brain.

2. A cyclopic eye is imperfectly formed, and therefore blind.

3. The cyclops eye both in single and double monsters is formed from the lateral portions of the common rudiment of two eyes which have grown forward in continuity with one another, the central parts being defective.

4. A cyclops eye is not formed by the fusion of two more or less fully developed optic cups but from a continuous area of the neural ectoderm which has failed to undergo the normal development into separate right and left optic vesicles. Varying degrees of the condition ranging from a single eye contained in a single orbital cavity, to only a slight approximation of the two eyes, may be explained by a more or less complete failure in the growth of the central parts of the common *primordium* from which the two optic vesicles are normally developed. If the defect in growth affects the whole of this area, there will be neither eyeball nor optic nerve, and the condition

may be accompanied by varying degrees of approximation of the external auditory meatuses leading up to a single median tympanic membrane and agnathia.

Two lenses contained within a single eyeball, will be due to two separate ectodermal invaginations into the mouths of an optic vesicle which is only partially subdivided, and there will be two *corneae* and two *irides*. If a single lens is found in a cyclops eye, it will be formed from a single ectodermal invagination and it will correspond to the outer halves of two lenses, which will be developed in continuity with one another over the brim of a composite optic cup. A constriction in the median plane has sometimes been observed in such double-lenses indicating their mode of origin. In other words as expressed by Schwalbe, a double-structured lens in a single eye does not prove that the rudiments of the lens are secondarily united, but the condition may be explained on the assumption that a certain degree of doubling of the optic cup has led to the development of two lens components.

5. As pointed out by Spemann and Schwalbe, the very great regularity of the double structures in these monsters, would be incomprehensible if the fusion theory were correct. If fusion were to take place one would expect with much greater probability considerable deformation due to opposed lateral pressure.

6. Cyclopia, and the various stages leading up to the complete condition, when occurring in a single monster, is, we believe, due to a "*general*" rather than a "*local*" or "*mechanical*" cause, such as pressure of the head-fold of the amnion, or too early union of the medullary folds, preventing inrolling of the intervening ectoderm to form the nasal halves of the two optic cups (Dareste).

7. It is possible, that a deleterious condition (acting) generally may affect one part more than another at a particular stage of development, owing to certain organs which are passing through a critical phase in their development being specially susceptible to such influences at that stage in their growth. Also owing to inequality in the rate of growth of certain parts of the embryo as compared with others any general interference in the growth of the embryo at a particular time would have a greater effect on the more rapidly growing parts than it would on those which at the time are growing less rapidly.

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THE ANATOMY OF A SYMELIAN MONSTER

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The number of recorded cases of monsters of the type to be described in this paper is not so large as might reasonably be expected, and no really satisfactory theory has been propounded to explain their occurrence.

The foetus which forms the subject of this note was born during the early part of the eighth month and belonged to the class of Symeles (Saint-Hilaire (1)). The head, arms and upper part of the body were well developed and, outwardly, normal, but the lower limbs were united to one another almost

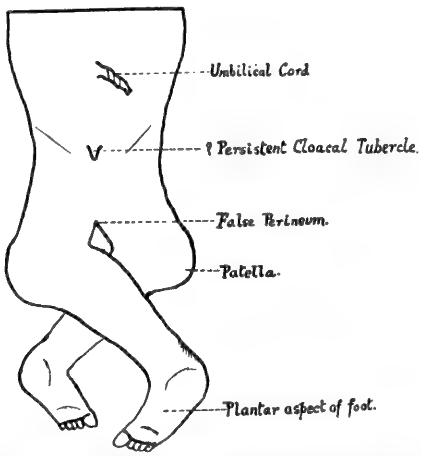

Fig. 1. Ventral view of lower half of Symelian Monster. The thighs are partially fused, the knees are directed laterally, the tibiae are anterior and the plantar aspect of the foot is directed forwards.

down to the knees, and both were rotated laterally (fig. 1). In addition, the buttocks did not show the usual prominence. The fused limbs possessed an unusual degree of mobility on the trunk. The hip-joints were practically fixed but the movement occurred in the lumbar region, where, as will be described later, an unusual joint was present.

No genito-urinary or anal apertures were present and the only representative of the external genital organs was a small, median, conical elevation, situated on the ventral aspect about midway between the umbilicus and the apparent perineum (fig. 1). It strongly suggested a penis, but it was imperforate and had no trace of a prepuce. On microscopical examination it was

found to consist of a core of connective tissue with a complete covering of skin, in which there were numerous hair follicles. No trace was found of an urethral plate and there were no vestiges of preputial folds.

The umbilical cord was normal in position and appearance, but it contained only two vessels, viz. the umbilical vein and a single umbilical artery.

It may be here stated that the degree of fusion of the lower limbs was less in the present case than in any other I have been able to trace, including the case recorded by Katz (14).

A summary of the abnormal conditions found in the various systems is given below, but detailed description is restricted to those points which appear to have an important bearing on the production of this type of monster.

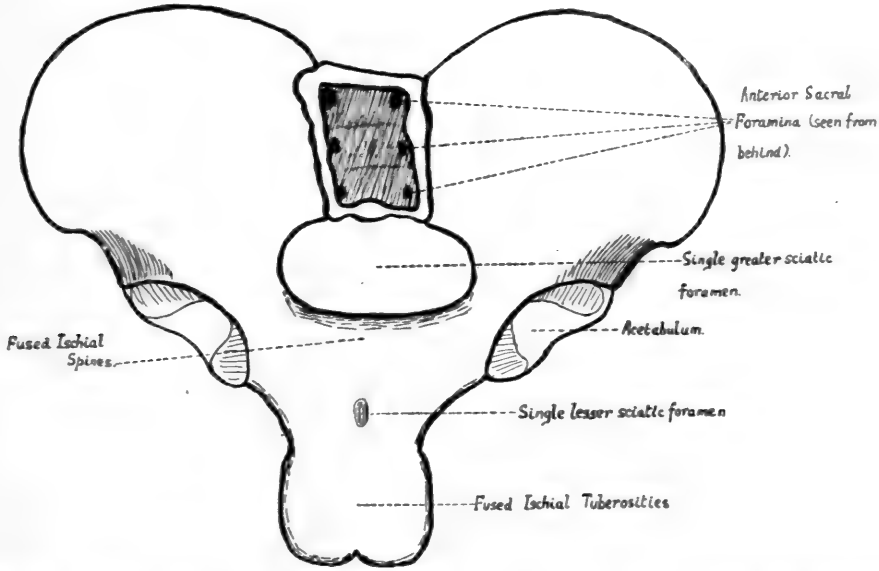

Fig. 2. Posterior view of the pelvis and sacrum. The sacrum is much reduced, and the ischia are fused in the regions of the ischial spines and in the regions of the tuberosities. The acetabula look backwards as well as downwards and laterally.

Osseous System. In this system, the anomalies were confined to the vertebral column, the ribs, the sternum and the innominate bones.

There were seven cervical, thirteen rib-bearing vertebrae and one lumbar vertebra. The sacrum was very rudimentary and consisted of three partly ossified vertebrae and a small cartilaginous nodule, which was all that represented the fourth and fifth pieces of the sacrum and the coccyx. As will be seen from fig. 2, a condition of spina bifida was present.

The bodies of the vertebrae showed few striking changes but neighbouring laminae were sometimes fused to one another, as were neighbouring transverse processes. The single lumbar vertebra had no vertebral arch and a large joint cavity was interposed between it and the sacrum. This accounted for the

unusual degree of movement between the lower limbs and pelvis, on the one hand, and the vertebral column, on the other. A similar condition has been recorded by Gebhard (2), but, as the lumbar vertebrae and the lumbo-sacral joint were normal in many of the cases described by other authors, the condition must be regarded as secondary. It represents an abnormal type of the normal flexion of the foetal limbs "in utero" and is probably to be attributed to limitation of movement at the hip-joints.

Neighbouring ribs, like the laminae and transverse processes of the thoracic vertebrae, showed a marked tendency to fuse, but only the dorsal portions were affected, the ventral portions remaining separate. There were thirteen ribs on the right side, and fourteen on the left side.

The innominate bones were separated posteriorly by the rudimentary sacrum. The ischia were fused to one another in the regions of the spines and again in the regions of the tuberosities. As a result, the greater sciatic foramina were thrown into one, and, at a lower level, a small median opening represented the fused lesser sciatic foramina. Median sagittal section showed that the pubes were fused to one another from the symphysis down to the ischia.

Muscular System. The psoas major, the glutaeus maximus, the piriformis, the gemelli and the obturator internus muscles all showed varying degrees of abnormality, but the most interesting anomaly was found in the biceps femoris. On both sides the short head was normal, but the long head, on the left side, arose from the fused tuberosities extending to the right of the middle line. On the right side, the long head was absent, but, in view of the fact that the long head of the left side was innervated both by the left and right sciatic nerves, it may be concluded that, in reality, it had fused with its fellow. On the other hand, the two semitendinosus muscles were quite separate, while the semimembranosus muscles, though quite independent at their origins, were partially blended for a short distance and then separated again.

Nervous System. Owing to the condition of the vertebral column, the spinal medulla was in two portions. The upper part ended opposite the lowest rib-bearing vertebra, while the lower part lay in the unclosed sacral canal.

The cervical and brachial plexuses were normally constituted, but, while there were thirteen intercostal nerves on the left side, there were only twelve on the right side. The lowest intercostal nerve, on each side, gave origin to the subcostal nerve and the upper root of the genito-femoral nerve.

There were no recognisable lumbar nerves, but there were three sacral nerves. S 1 was a large nerve, which gave origin to the lower root of the genito-femoral, the lateral cutaneous nerve of the thigh, the femoral and the obturator nerves and, in addition, sent a communicating branch to S 2. The latter, further strengthened by a branch from S 3, formed the sciatic band, while the remainder of S 3 constituted the posterior cutaneous nerve of the thigh.

Circulatory System. The only striking anomalies discovered were found in the abdomen. There was, as is usual in these monsters, a single, median umbilical artery, directly continuous with the abdominal aorta. The common iliac arteries were therefore indistinguishable, but the external iliacs arose by a common trunk from the dorsal aspect of the single median artery and almost at once separated, being normal in the remainder of their course so far as could be traced. Their common trunk gave off a few small branches to the rudimentary pelvis and a single gluteal artery on each side.

The inferior mesenteric artery was absent.

There were no striking anomalies present in the veins.

Abdominal Viscera. The stomach, the duodenum and the rest of the small intestine were normal, as were the liver, spleen and pancreas. The large intestine ended blindly in the region of the spleen, and was considerably

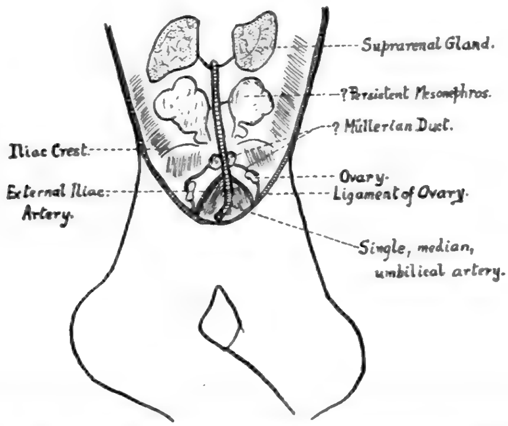

Fig. 3. Structures on the posterior abdominal wall, showing the single, median, umbilical artery

distended with meconium. It was supplied, in its whole extent by the colic branches of the superior mesenteric artery.

The suprarenal glands were normal.

The kidneys were absent, but occupying their position on the posterior abdominal wall were two flattened, partly lobulated structures which extended downwards as far as the iliac crests (fig. 3). Microscopical examination showed that these structures contained a tube, but the characters of its epithelial lining could not be determined owing to imperfect fixation. The wall of the tube contained a thick layer of unstriped muscle, and, in some sections what looked very like degenerated glomeruli were observed. I believe that this structure is a remnant of the mesonephros and its duct.

The ureters and bladder were absent.

The ovary lay in the iliac fossa. It had a normal relationship to the uterine tube and the meso-salpinx, but the uterus, as such, was absent. The uterine tube passed backwards and medially and became continuous, on each side,

with a small nodule which lay near the abdominal aorta (fig. 3). This nodule, on section, consisted of a strong muscular wall containing a tube in its centre. On microscopical examination, it was possible to identify the lining epithelium of the tube as being columnar in character, but it was impossible to determine whether or not it had been ciliated. These nodules represent the unfused Mullerian ducts.

The ligament of the ovary was, in the absence of the uterus, directly continuous with the round ligament and, after traversing the inguinal canal (fig. 3), terminated in the subcutaneous tissue over the pubis.

As already indicated, the colon was absent below the left colic flexure.

To sum up, the most striking anomalies were the following:

(*a*) Partial fusion of the skin, fasciae and muscles of the thighs.

(*b*) Fusion of ischia and pubes.

(*c*) Presence of a single, median, umbilical artery.

(*d*) Rudimentary condition of the sacrum, absence of coccyx and disappearance of four lumbar vertebrae.

(*e*) Absence of terminal portion of colon.

(*f*) Absence of kidneys, ureters, bladder and urethra.

(*g*) Vestigial character of external genitalia.

(*h*) Presence of femoral, obturator nerves, etc., despite the absence of the lumbar nerves and the lumbar part of the spinal cord.

(*i*) Partial fusion of vertebral arches and ribs, asymmetrically.

(*k*) Innervation of the long head of the left biceps femoris by both sciatic nerves.

In monsters of the type just described, the most striking deformity is the fusion of the lower limbs and it was the fact that the degree of fusion is subject to great variation that led Saint-Hilaire (1) to suggest the following grouping: (1) Symeles, in which fusion has not affected the feet; (2) Uromeles, in which, in addition to fusion of the limbs, the feet are fused into one; (3) Sirenomeles, in which the two limbs fuse to form a stump, no foot being present. This subdivision, however, is not of great value as it only takes account of one of the features constantly found in these monsters.

A complete review of the earlier literature on the subject was given by Manners-Smith (4) in 1895. Since then, Mall (5) has shown that "pathological embryos, experimental monsters and human monsters at term form a class by themselves, inasmuch as they are produced from normal ova through causes which lie in their environment." This observation at once discounts the views as to the origin of the Symelian and allied monsters put forward by Gebhard (2), Vrolik (6) and others. Saint-Hilaire's (1) view, which Manners-Smith (4) felt compelled to fall back on, is unsatisfactory in that, although one naturally agrees with the statement that, given the opportunity, symmetrically developed structures tend to fuse with one another, it fails to suggest any reason for the origin of the conditions favourable to fusion.

As a result of the varied conditions found in this group of monsters, anomalies, which, though interesting in themselves, are relatively unimportant because inconstant, have frequently been described in great detail, whereas anomalies, which are of great importance because they are constant, have frequently received scant attention. It is only by a close study of the constant features that one can hope to arrive at the exciting cause of the malformation. The following list has been drawn up from a study of the available literature.

(1) There is always present a single, median umbilical artery in direct continuity with the abdominal aorta.

(2) There is always some degree of fusion of the lower limbs. This condition varies from that found in the present case to that found in Sirenomeles (Moorhead (12), etc.).

(3) There is always some degree of suppression at the caudal end of the vertebral column.

(4) There is always some degree of interference with the development of the cloaca and the external genitalia.

(5) So far as has been discovered, the head, neck, upper limbs and thoracic viscera are usually normal.

Of these features, I believe that the first is the most worthy of consideration. Its constancy was early noted but its importance has been, to a large extent, overlooked. Solger (7), whose views are quoted by Manners-Smith (4)—I have been unable to obtain his original paper—pointed out that the single umbilical artery was not the persistent member of a pair but was formed by fusion of the two umbilical arteries. When they are first recognisable in the human embryo, the umbilical arteries are represented by arterial plexuses spreading over the sides of the caudal end of the yolk-sac, connected dorsally at several points with the tailward continuations of the aortae. Fusion of these two plexuses caudally would result, firstly, in the production of a single, median, umbilical artery continuous with the abdominal aorta, and, secondly, in the formation of an obstruction to the tailward growth of the hind-gut and to the development of the cloacal membrane. This arrangement would be in keeping with the described conditions of the structures whose development is dependent on the growth of the hind-gut and the formation of the cloacal membrane, since the large intestine ends blindly, and the bladder, urethra, anal orifice and external genitalia are awanting in these cases.

It is perfectly clear that the converse of this proposition might be stated, namely that failure of the hind-gut to develop would permit the umbilical arteries to meet and fuse. Consideration, however, of cases described by Gebhard (2) and Manners-Smith (8) leads to the view that the failure of the cloacal development is secondary to the arterial fusion, and that the precise stage in the embryo at which this fusion is completed is open to some slight variation.

Gebhard (2) found a band of connective tissue passing from the ventral aspect of the blind termination of the large gut in company with the umbilical artery to the umbilicus. It contained a tube which communicated dorsally

with the large gut and which Gebhard identified, as I think correctly, as the "allantoisstiel." The persistence of the allantois in this case may be regarded as being due to the fact that the arterial fusion occurred or was completed at a slightly later stage than in the majority of cases.

Manners-Smith (8), in his third case, records that the rectum was present, but that it ended blindly both above and below and it received the deferent ducts. Further a small urinary bladder was present, but it possessed no openings into it or out of it. The conditions present in this case are very suggestive and they indicate, to my mind, that fusion of the umbilical arteries was not completed till the cloaca had reached a stage of development similar to that seen in the human embryo of 4·25 mm. vertex-breech length, figured by Felix (9). It is obvious that, since the deferent ducts open into the rectum, the urorectal septum has not been responsible for the subdivision of the cloaca and I believe that fusion of the umbilical arteries, completed at a stage such as has been suggested, would account for the conditions found in this case quite satisfactorily.

On the other hand, the case recorded by Abramov and Rjesanov (3) presents a difficulty which is not easy to explain. They record the presence of a tail-like process in the sacral region, traversed by a canal, which opened to the exterior near the end of the tail and was connected to the dorsal wall of the large gut. The bladder and external genitalia were absent and there was the usual single, median, umbilical artery. The authors regard the external opening on the tail as the anus, but, from the description given by them, it is certain that the orifice does not represent the true anus. Unless the connection with the large gut was an artefact produced by the metal sound used to explore the canal in the tail, then, whether it be a patent neurenteric canal or a true portion of the gut, the fusion of the umbilical arteries cannot have been complete. It should be stated that the authors, relying on a case—not a Symelian monster—described by Weigert (10), identify the umbilical artery as a persistent omphalo-mesenteric artery. Weigert's description is far from convincing and there is little doubt that the artery, identified by him as a persistent omphalo-mesenteric artery and held by him to be identical with the single umbilical artery of Symelian monsters, was in reality the right umbilical artery, the left umbilical having failed, as it sometimes does.

The fusion of the lower limbs is a condition referable to a slightly later stage than that at which the fusion of the umbilical arteries takes place and it can only occur in the absence or reduction of the structures which normally intervene between them, i.e. the cloaca and the caudal end of the vertebral column. Manners-Smith's (8) case, quoted above, shows that the latter is the more important factor. Narrowing of the tail end of the embryo due to reduction of the vertebral column is to be regarded as probably due to deficiency in the vascular supply. Such a narrowing causes approximation of the lower limb buds, post-axial border to post-axial border and, in high degrees of fusion, it is found that the fibulae fuse with one another, while the tibiae

remain separate. The degree of fusion of the limbs apparently depends on whether the two limb buds at their first appearance possess a common post-axial border or whether, originally separate, the post-axial borders meet at the bases of the buds as they enlarge with the elongation of the limbs. In any case, it is certain that the degree of fusion is determined very soon after the appearance of the buds. As a result of fusion, the limbs are anchored to one another and normal rotation fails to occur.

Under normal conditions, the sclero-blastema does not appear in the lower limb bud until the embryo has reached a length of 9 mm. (Bardeen (11)) and at that stage the sacral and the upper two coccygeal vertebrae are already laid down. Further, before the ischial and pubic processes are recognisable, the vertebral column has elongated considerably. It is clear, therefore, that the failure of development of the vertebral column must precede the fusion of the lower limbs and this developmental failure, as already indicated, probably has its cause in vascular deficiency.

Whether this latter is attributable in any way to the fusion of the umbilical arteries, or whether both are referable to some still earlier common cause, it is impossible to say without further evidence and that evidence can only be obtained by the careful examination of further cases. The most that can be said at present is that the single median umbilical artery and the reduction at the lower end of the vertebral column are the true primary anomalies, and that the fusion of the limbs and the failure of the bladder, etc., to develop are subsidiary to them.

It is not my intention to discuss the numerous other interesting anomalies which were found in this monster, since, as I have shown, they cannot be regarded as throwing any light on the general condition.

In conclusion, I desire to express my indebtedness to Professor Arthur Robinson, through whose kindness the specimen came into my possession.

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SEXUAL DIMORPHISM IN *RANA TEMPORARIA*, AS EXHIBITED IN *RIGOR MORTIS*

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In December last I had occasion to separate the males from the females among the frogs which had been killed and distributed for the Practical Zoology class in the University of Edinburgh. Eighty-five common frogs (*Rana temporaria*) had been killed, half an hour before I saw them, by immersion in liquid chloroform, and had been placed in the water of the dissecting-dishes.

I anticipated no difficulty in recognising the sexes, for in specimens of a size suitable for dissection, the sexual differences are fairly obvious even on casual inspection. The male presents a general appearance of 'maleness,' suggesting sturdy compact strength; the limbs, and particularly the fore-limbs, are massive with well-developed muscles; the trunk is squarish in outline, and the abdominal muscles are so thick that through them the viscera cannot be identified; and the skin of the back and flanks is comparatively smooth. The female, on the other hand, is much more slightly built and her limbs are more slender and not nearly so muscular; through the thin abdominal wall the pigmented ovaries can be seen distinctly, during a great part of the year, and at all times, the development of the internal reproductive organs is sufficient to produce a bulging of the flanks and a suggestion of fullness of the abdominal cavity; and during the breeding-season the skin of the back and flanks becomes roughened in consequence of the development of the temporary papillae. In December, however, these are not sufficiently developed to produce this typical roughness.

But for my decision as to which were males, I meant to depend upon the presence of the finger-pad. Upon the palmar surface of the innermost finger, the index, of the male frog, is found a cushion or tubercle, which takes the form of a rounded, oval swelling, black or deep-brown in colour, during the breeding-season, and grey at other times.

But a rapid inspection of the frogs at once indicated that this test was inapplicable, for, as they lay in the stiffness of death, about half their number had assumed an attitude in which the palms of the hands were tightly hidden from view and could not be exposed without fracture of bones and tearing of muscles. These were collected and examined. The attitude of every one of the whole forty was identical in every particular, and every one was undoubtedly a male. The other forty-five were collected and compared, and it was seen that they were female, one and all, and that the attitude assumed by them was similar in every case; and further it became clear that in *rigor mortis* there was

such a difference in the attitudes assumed by the male and by the female, that the sex could be told at a glance. Further consideration showed that this difference in attitude depicted in a most striking way the sexual dimorphism that exists in the common frog.

The finger-pad undoubtedly marks the male, and the roughened back denotes the female; but the most notable external differences which distinguish the sexes, are those which depend upon the underlying differences in the degree

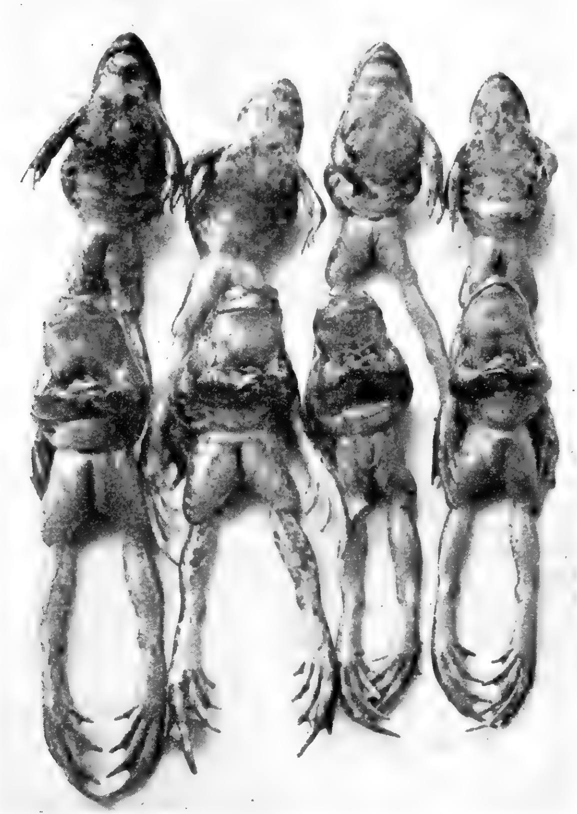

Fig. 1. The upper row are females, the lower, males.

of development of three muscles, which to the male are of supreme importance during the breeding-season. These muscles are the *rectus abdominis*, the *flexor carpi radialis*, and the *abductor indicis longus*, and in the male they attain a considerable degree of development, being always of a much greater size than the same muscles of a female of the same age. During the breeding-season they become even larger still in the case of the male, and it is to these muscles, that the differences in appearance, which the sexes exhibit, both in life and during *rigor mortis*, are due.

I. *M. rectus abdominis*

On either side of the middle line of the abdominal wall, and separated from its fellow of the opposite side by the fibrous *linea alba*, is found this long flat muscle, broadest in its middle part, which arises by a narrow strong tendon, from the inferior border of the pubis, and runs forwards to divide at the level of the second of the five *inscriptiones tendineae*, counting from behind forwards, into two portions. The outer portion forms the *portio abdominalis* of the *m. pectoralis*, whilst the inner portion is continued as the *rectus abdominis*, which, narrowing as it approaches the pectoral girdle, divides so that the median fibres are inserted into the cartilaginous plate of the xiphisternum, and the rest are continued into the *m. sternohyoideus*.

The *m. pectoralis* covers the ventral surface of the pectoral girdle and consists of three portions, of which the largest and strongest is the *portio abdominalis*, which is the direct continuation of the outer portion of the *m. rectus abdominis*. This portion is inserted into the median surface of the *crista ventralis humeri*. The *m. sternohyoideus* has two origins, an inner, from the upper surface of the inner extremity of the coracoid and from the *pars cartilaginea* and *pars ossea sterni*, and an outer, which is the direct continuation of the *m. rectus abdominis* in front of the fifth *inscriptio*. The muscle passes forwards on the upper surface of the coracoid and of the clavicle, and during its course its direction abruptly changes from the horizontal to the vertical as it dips to pass between the two insertions of the *m. geniohyoideus* to become inserted into the lower surface of the hyoid and its posterior cornu.

The action of the *m. rectus abdominis*, when both girdles are fixed, is to shorten and tense the abdominal wall, and so to compress the viscera, thus assisting to evacuate the excretions from the cloaca and bladder, and the products of the internal reproductive organs from the seminal vesicles or oviducts and from the cloaca. When neither girdle is fixed, contraction of the muscles of both sides working in unison, will produce flexion of the vertebral column. The *m. pectoralis* adducts the arm, bringing it across the chest, and at the same time rotates it inwards. The *m. sternohyoideus* is a depressor of the hyoid. The action of the *m. rectus abdominis* and its continuations is countered by that of the extensor group of muscles of the dorsal aspect of the vertebral column, particularly the *m. longissimus dorsi, ileolumbaris, dorsalis scapulae, latissimus dorsi* and *geniohyoideus*.

II. *M. flexor carpi radialis*

The site of origin of this muscle upon the humerus is marked, in the case of the male, by a well-defined crest, the *crista medialis*, near the *epicondylus medialis*. This crest is not present in the female, whilst in the male its great development is made necessary by the much greater size of the muscle. Narrowing as it courses down the forearm, the muscle is inserted into the median prominence of the *os centrale*. Its action is to flex the forearm and wrist but it is particularly concerned with the movement of the hand and wrist

lateralwards to the thumb-side, and so plays an all-important rôle during the sexual act. In the male, this large muscle becomes even larger during the breeding-season, but at all times it is bigger and more powerful in the male than in the female.

III. *M. abductor indicis longus*

This muscle arises from the lateral surface of the *os antibrachii* (*caput inferius*); from the *epicondylus lateralis humeri* (*caput superius*); and from the radius (*caput breve*), and passes obliquely down the forearm and over the wrist-joint to be inserted into the metacarpal of the second digit which serves as a thumb. In the male, this metacarpal is much stronger and stouter than in the female, and on its inner aspect a ridge is developed to provide for the insertion of this muscle, which becomes much enlarged during the breeding-season. The action of this muscle carries the second digit lateralwards away from the rest of the hand, and causes it to press firmly against the chest of the female during the sexual act.

As for the rest of the muscles, it is found that those of the male are somewhat larger than those of the female of the same size, but not sufficiently so to be at all indicative of the sex. The angle which the legs make one with the other is bigger in the female than in the male, but its size varies too much to permit a generalisation such as this to be regarded as a sex-difference.

Combined and full action of these three muscles, the much greater development of which is a male characteristic, will cause the body to assume the following attitude. The head will be flexed upon the chest and the floor of the mouth depressed (*m. rectus abdominis* and *sternohyoideus*). The vertebral column will be flexed and the abdominal wall concave and tense (*m. rectus abdominis*). The arms will be adducted and rotated inwards, so that they will be brought across the chest (*m. rectus abdominis* and *pectoralis*). The forearms will be flexed and pressed against the chest-wall (*m. flexor carpi radialis*). The wrists will be flexed (*m. flexor carpi radialis*). The index finger will be abducted strongly (*m. abductor indicis longus*). So that the palms of the hands will be held together, the fingers interlocked, and the index finger held well away from the rest of the hand.

And this is the very picture that the males presented as they lay in *rigor mortis*, whilst the attitude of the females demonstrated, that in them, there was no special degree of development of any particular muscles, although it did seem that the ventral muscles were weaker than the dorsal, for the attitude assumed was one of general extension.

There is nothing remarkable in the fact that, in a case such as this, where the sexual dimorphism rests on differences in the degree of the development of some certain muscles, the differences in the external appearances of the sexes will be most strikingly depicted in the attitudes of *rigor mortis*. For during this phase of tonic contraction, when the interaction of opposing muscles is deciding the posture which the body shall adopt, such muscles as

the three described above, will exert an overwhelming force, swamp all opposition, and dictate what this attitude will be.

In the case of the frog, this illustration of the sexual dimorphism is particularly striking, and it would appear that only the cloak of familiarity could have screened from others the picture which revealed itself to me by chance. It seems probable that, if in December this difference in attitude in *rigor*

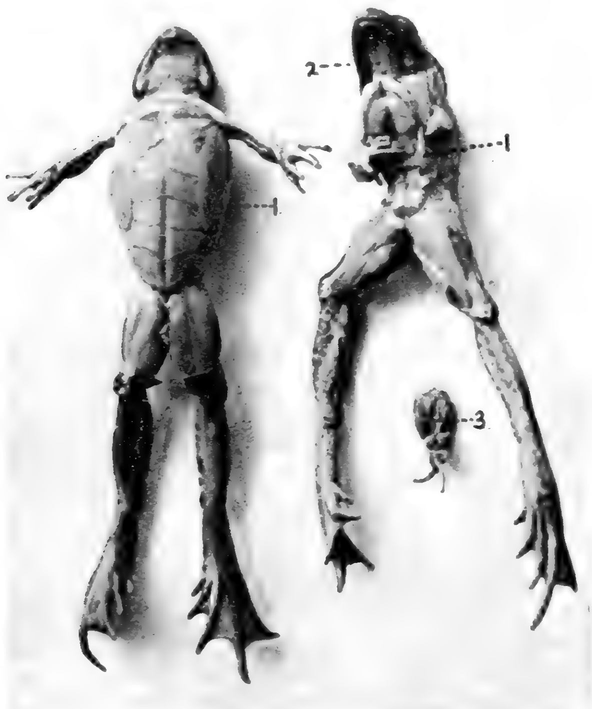

Fig. 2. Male and female forms contrasted.

1 = the continuation of the *m. rectus abdominis* which constitutes the *portio abdominalis* of the *m. pectoralis.*

2 = the continuation of the *m. rectus abdominis* which constitutes the greater part of the *m. sternohyoideus.*

3 = the left forearm and hand of the male. This shows the great size of the muscles of the forearm, particularly of the *m. flexor carpi radialis*; and the position of the index finger.

mortis is exhibited, it will occur at all times of the year. It is entertaining to wonder if, in the human, certain trades, which call out a predominating development of certain groups of muscles, cannot be told by the attitude of the body in *rigor mortis*, and if in other species, sexual dimorphism is as well portrayed as in the case of the frog.

In figure 1, it will be seen that the upper row is of females, and the lower one of males. Figure 2 shows a male and a female dissected to demonstrate the difference in the degree of development of the muscles.

THE CONSTRICTOR MUSCLES OF THE BRANCHIAL ARCHES IN ACANTHIAS BLAINVILLII

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In my work on "The Homologies of the Muscles related to the Visceral Arches of the Gnathostome Fishes" (Allis, 1917), I came to the conclusion that there must have been, primarily, some overlapping of the constrictores superficiales in the branchial arches of Acanthias, and that if that condition persisted, and if the innervation of these muscles was as given by Vetter (1874), Tiesing (1895) and Ruge (1897), these muscles would present typical examples of a muscle derived from one segment of the body and innervated by the nerve of another segment.

I have since then received some specimens of Acanthias blainvillii, and have had the muscles and their innervation traced by my assistant, Mr John Henry. The drawings are by Mr Jujiro Nomura, and the veins, arteries and nerves are, because of the reproduction in black and white, shown considerably enlarged. This is particularly true of the terminal branches of the nerves, which are, of course, very delicate.

When the skin of this fish is removed in the branchial region, it leaves a thin subdermal fascia-like layer of connective tissue, which is loosely attached to the inner surface of the skin and is closely applied to the outer surface of the constrictor muscles. Enclosed within this tissue there is a series of dorso-ventral veins, which are connected by others which run longitudinally or diagonally. The anterior one of the dorso-ventral veins arises from the superior jugular vein, and runs downward along the line between the larger, posterior portion of the constrictor superficialis dorsalis of the hyal arch and an anterior portion of that constrictor which is inserted on the hyomandibula. At the ventral end of the latter muscle the vein turns posteriorly and then anteriorly along the dorsal and ventral edges of the large triangular aponeurosis that lies between the dorsal and ventral portions of the constrictor of the hyal arch and is described by both Vetter and Marion (1905), and then turns downward along the posterior edge of the muscle Csv_1 of Marion's descriptions, between it and a band-like muscle bundle that is called by Marion the muscle Csv_{1a}, and falls into the inferior jugular vein. The next posterior vein arises from the superior jugular, runs downward along the dorsal aponeurotic line related to the first gill opening, passes along the posterior edge of that opening, and then onward along the corresponding ventral aponeurotic line, and falls into the inferior jugular. The next three posterior veins have similar origins and similar relations to the aponeurotic lines related to the second, third and fourth

gill openings, and each falls, ventrally, into the inferior jugular. Posterior to these five veins there is a sixth one which arises from a dorsal longitudinal commissural vein, described immediately below, and runs downward along the hind edge of the muscle Csd_6 until it reaches the dorsal edge of the fifth gill opening, where it turns outward on the dorsal surface of the base of the pectoral fin. Approximately parallel to that part of this vein that lies in the base of the pectoral fin, but lying on the ventral surface of that fin, there is another vein which leaves the fin approximately at the ventral edge of the fifth gill opening, and from there runs downward along the hind edge of the muscle Csv_6, and falls into the inferior jugular; these two veins, together, thus forming a vessel similar to those related to the anterior gill openings, excepting in that it does not arise from the superior jugular and that it is interrupted as it runs around the hind edge of the gill opening to which it is related. Posterior to this vein a seventh one arises either from the base of the superior jugular vein, or from the sinus venosus, and is distributed to the pectoral fin, this vein having the appearance of being a serial homologue of the more anterior ones but not being connected ventrally with the inferior jugular.

These several veins are all connected with each other by a dorsal longitudinal commissure which runs posteriorly along the ventral edge of the musculus trapezius and then across the external surface of the shoulder-girdle, the sixth vein of the series arising from this commissure and not from the superior jugular. Ventral to this dorsal commissure, about half way between it and the gill openings, a second longitudinal commissure connects the posterior six veins. Immediately dorsal to the gill openings still another longitudinal commissure extends from the second to the sixth vein; and dorsal to this commissure the posterior five veins are connected with each other by a number of other commissural vessels which have a dorso-posterior, and hence diagonal course. Ventral to the gill openings the second to the sixth veins are connected with each other by a ventral longitudinal commissure which lies along the ventral edge of the muscle-sheet formed by the constrictores superficiales of the several arches.

Accompanying each of the dorso-ventral veins related to the five gill openings, but lying internal to them and the enclosing tissue, directly upon the related linear aponeuroses, there are dorsal and ventral arteries the origins of which will be given later. Each of the dorsal arteries extends downward almost to the dorsal edge of the related gill opening, the ventral arteries each extending upward, posterior to the related gill opening, to its dorsal edge, but not apparently there connecting with the dorsal artery.

When these veins and arteries, and the related tissue, have been removed, the constrictores superficiales are exposed, these muscles forming what appears to be a practically continuous muscle-sheet crossed by the four well-known aponeurotic lines, which extend dorsally and ventro-mesially from each of the first four gill openings.

The dorsal portion of the constrictor of the mandibular arch was not

examined. The ventral portion consists of a musculus intermandibularis and, posterior to it, on either side, a sheet-like muscle (Csv_1), which has its origin on the mandible and its insertion on a median aponeurosis common to it and its fellow of the opposite side. These two muscles form a continuous sheet innervated by branches of the ramus mandibularis trigemini, and hence are parts of the constrictor superficialis of the mandibular arch, as Marion, who describes them both, concluded. Vetter did not find an intermandibularis in this fish, and he calls the sheet-like muscle the muscle Csv_2, thus assigning it to the hyal arch.

Beneath the muscle Csv_1, there is a second sheet-like muscle, most of the fibers of which have their origins on the ceratohyal but a few posterior ones on the hyomandibula. The fibers of the muscle radiate somewhat, the anterior ones running antero-mesially and the posterior ones postero-mesially. All these fibers are inserted on a deeper portion of the median aponeurosis that gives insertion to the superficial muscle Csv_1, the anterior fibers not extending as far mesially as the posterior ones. This deeper muscle is innervated by branches of the ramus hyoideus facialis and hence is, as Marion states, a part of the constrictor of the hyal arch. It is accordingly an interhyoideus, and may be so referred to. Superficial to its posterior portion there is a narrow muscle-bundle which is the muscle Csv_{1a} of Marion's descriptions. It arises on the outer surface of the musculus adductor mandibulae, runs postero-mesially along the hind edge of the muscle Csv_1, and is inserted on a posterior portion of the median aponeurosis that gives insertion to the latter muscle and the interhyoideus. This muscle bundle has the appearance of being a posterior portion of the muscle Csv_1, but it is innervated by branches of the ramus hyoideus facialis, the branch that innervates it running forward internal to the bundle, outward along its anterior edge, between it and the muscle Csv_1, and then posteriorly across the external surface of the bundle on to the external surface of the muscle Csv_2. At the point where it turns posteriorly, a sensory branch is given off, which runs anteriorly and anastomoses completely with a terminal branch of that branch of the ramus mandibularis trigemini that innervates the muscle Csv_1, this relation of these nerves thus being as in Amia and many of the Teleostei. This muscle bundle is thus a part of the constrictor of the hyal arch, and not, as Marion concluded, of the mandibular arch. It apparently corresponds to the musculus depressor rostri of the Batoidei, but as that term is here inappropriate it may be called the muscle Csv_{2a}.

Corresponding to these two parts of the ventral portion of the constrictor of the hyal arch, the anterior fibers of the dorsal portion of the constrictor form a band-like muscle which has its origin in the fibrous fascia that covers the outer surface of the trunk muscles, and running ventro-anteriorly has its insertion mainly on the hyomandibula but partly also on the palatoquadrate, these two parts of this muscle being found as distinctly separate muscles in one of two specimens that were examined. This muscle is the homologue of the levator hyomandibularis of the Batoidei, and may be so designated.

The remainder of the constrictor of the hyal arch forms a large flat muscle sheet, Cs_2, which fills the space between the hind edges of the dorsal and ventral muscles above described and the articular ends of the palatoquadrate and mandible, anteriorly, and the first gill opening and the related linear aponeuroses posteriorly, and extends, both dorsally and ventrally, beyond the latter aponeuroses. The larger part of this muscle is cut into dorsal and ventral portions by the large triangular aponeurosis, above referred to, that extends posteriorly from the articular ends of the palatoquadrate and mandible. This aponeurosis lies directly upon the branchial rays of the hyal arch, has quite certainly been formed in relation to them, and has its counterpart in the several aponeurotic lines formed where the fibers of the musculi interbranchiales of the branchial arches cross the branchial rays of the related arches. Posterior to the pointed hind end of this aponeurosis, between it and the anterior edge of the first gill opening, the fibers of Cs_2 have a dorso-ventral course and are inserted dorsally on the dorsal linear aponeurosis related to the first gill opening and ventrally on the corresponding ventral aponeurosis.

Anterior to these dorso-ventral fibers of Cs_2, the dorsal and ventral fibers of the muscle may be said to arise, respectively, from the dorsal and ventral edges of the large triangular aponeurosis, and they are connected, across the aponeurosis, by ligamentous lines in relation to which small isolated muscle bundles may be found. The dorsal fibers run dorso-posteriorly, the anterior (proximal) ones lying parallel to, and in contact with, the hind edge of the levator hyomandibularis. An important bundle of the anterior fibers of the muscle pass, because of their dorso-posterior direction, dorso-anterior to the dorsal end of the aponeurotic line related to the first gill opening. These fibers become tendinous at their dorso-posterior ends and are there gathered into a muscle-head which either passes ventral to the ventral edge of the anterior end of the musculus trapezius, or perforates that edge, and is inserted in the fascia that covers the trunk muscles. Posterior (distal) to these fibers, an equally important bundle separates into superficial and deeper layers. The deeper layer is inserted on the linear aponeurosis related to the first gill opening, none of them apparently having their insertion on the underlying extrabranchial. The superficial layer passes external to that aponeurosis, between it and the overlying vein, and is enclosed in a loop of the related artery, to be later described. The fibers of this layer then continue dorso-posteriorly, lying directly upon the anterior (proximal) fibers of the muscle Csd_3, and toward their dorso-posterior ends unite with the latter fibers to form a muscle bundle which contracts to a tendinous muscle-head and perforates the ventral edge of the musculus trapezius dorsal to the dorsal end of the linear aponeurosis related to the second gill opening, and has its insertion in the fascia that covers the trunk muscles. Posterior (distal) to these fibers, the remaining fibers of this part of the muscle all have their insertions on the linear aponeurosis related to the first gill opening.

The ventral portion of Cs_2 is strictly comparable to the dorsal portion.

Its anterior edge lies parallel to, and in contact with, the hind edge of the muscle that I have called the muscle Csv_{2a}, but not in contact with that edge of the musculus interhyoideus, lying somewhat posterior to it and, in one of two specimens examined, being connected with it by a number of separate muscle strands which lie internal to the muscle Csv_{2a}.

A few anterior fibers of Csv_2 separate ventrally from the remainder and are inserted on the median aponeurosis that gives insertion to Csv_{2a}. This bundle corresponds to that dorsal bundle of the muscle that perforates the ventral edge of the musculus trapezius dorso-anterior to the dorsal end of the linear aponeurosis related to the first gill opening, and also to what Vetter calls the deeper portion of the constrictor superficialis of Heptanchus. The next posterior fibers of Csv_2 separate into superficial and deeper bundles, the latter one having its insertion on the linear aponeurosis related to the first gill opening, and the superficial bundle passing external to that aponeurosis, between it and the related vein, and enclosed in a loop of the related artery, and being inserted, with the underlying fibers of the muscle Csv_3 in tissues along the lateral edge of the musculus coracoarcualis, the posterior fibers even passing across the linear aponeurosis related to the second gill opening.

The dorsal and ventral superficial bundles of Cs_2 are, as above stated, respectively enclosed in a loop of the artery related to the dorsal and ventral linear aponeurosis of the first gill opening. The dorsal artery arises from the dorsal longitudinal commissure of the efferent branchial arteries, and runs outward along the dorsal extrabranchial of the first branchial (glossopharyngeal) arch until it reaches the dorso-anterior edge of the dorsal superficial bundle of Cs_2. There it separates into two parts, one of which runs ventrally internal to the bundle and the other external to it, the two branches uniting at the ventro-posterior edge of the bundle. There a branch is sent downward along the external surface of Cs_3, and goes to dermal tissues, the remainder of the artery running downward along the linear aponeurosis related to the first gill opening. The ventral artery arises from the ventral longitudinal commissure of the efferent branchial arteries, and forms a loop around the ventral superficial bundle of Cs_2 similar to the one formed by the dorsal artery around the dorsal superficial bundle. Each of these loops is connected by a commissural branch with a similar loop formed in relation to the superficial bundle of the muscle Cs_3, and that loop with similar loops formed by the arteries related to the third and fourth aponeurotic lines, dorsal and ventral longitudinal commissures thus being formed. Each superficial muscle bundle is indented where it is crossed by the related vein and artery, this indentation being slight for the ventral muscle but more marked for the dorsal one, the fibers of the latter muscle being partly cut through and the nerves that supply them pinched so that they are markedly thin at these points. The nerves and muscle fibers are certainly here injured by the pressure of the blood vessels, and as the muscles of this arch, and similar ones in the more posterior arches, vary greatly in size in different specimens, in some being reduced to only a few

strands, or even wholly absent, the conditions would seem to show that these superficial bundles are in process of abortion.

The dorsal and ventral aponeuroses on which the fibers of the several constrictor muscles have their insertions lie directly beneath the related blood vessels, as above stated, and along the antero-lateral edge of the gill pouch next posterior to the gill opening to which the aponeuroses are considered to be related. The dorsal and ventral aponeuroses of each arch lie parallel, and slightly anterior to, the extrabranchials of their arch, those extrabranchials thus lying in the roof of the next posterior gill pouch. The aponeuroses each extend beyond the related extrabranchial and each passes posterior to the gill opening to which it is considered to be related, the dorsal aponeurosis extending ventrally beyond the dorsal edge of that gill opening, and the ventral one extending dorsally beyond its ventral edge. The dorsal and ventral extrabranchials do not either of them extend to the corresponding edge of the gill opening. It thus seems certain that the aponeuroses were not developed primarily in relation to the extrabranchials but to the antero-lateral edge of the gill pouch next posterior to the arch to which the aponeuroses belong. In the action of respiration this pouch was continually expanding and contracting, and as it expanded it must have exerted pressure on the muscle that passed over its antero-lateral edge and so have given rise to an aponeurosis, the pressure of the blood vessels that overlie the aponeurosis doubtless contributing to its formation.

In the glossopharyngeus, or first branchial arch the primitive muscle-mass was first separated into adductor and constrictor portions in the manner explained in an earlier work (Allis, 1917). The distal (posterior) fibers of the constrictor portion then turned posteriorly both at their dorsal and ventral ends, and where they crossed the extrabranchials of their arch linear aponeuroses were developed, these aponeuroses lying external to those portions of the extrabranchials that lie distal to their sharply bent-in proximal ends. The aponeuroses accordingly started from the dorsal and ventral ends of the original constrictor, at points intermediate between their distal (posterior) and proximal (anterior) edges, and they cut the constrictor portion of the muscle of each arch into the so-called interbranchialis and constrictor superficialis. The fibers that were cut by the aponeuroses were, necessarily, primarily inserted on them, but they later acquired, in part, insertion also on the underlying extrabranchials. The fibers that lay wholly distal or proximal to the aponeuroses were not cut by them, and hence retained their full lengths.

The distal fibers of the interbranchialis accordingly have their dorsal attachments either on the aponeurosis that cuts this muscle out of the original constrictor, or on the underlying part of the dorsal extrabranchial of the arch. Proximal (anterior) to these fibers, the fibers are inserted mostly in fibrous tissues that surround the superior jugular vein, the distal ones lying upon the bent-in dorsal end of the extrabranchial of the arch and doubtless there being in part attached to it. These fibers all run ventrally, in a curved course,

and have their insertions on the ventral aponeurotic line related to the muscle, and on the underlying portion of the ventral extrabranchial of the arch, and they are crossed by a number of aponeurotic lines developed in relation both to the branchial rays of the arch and the posterior efferent artery, the rays lying against the posterior surface of the muscle and the artery posterior to the rays. The tips of the median and next ventral rays of the series perforate the muscle and project posteriorly along its anterior surface. In the ventral half of the muscle a large proximal portion of the fibers have their origins on the ceratobranchial of the arch, and hence do not form a ventral continuation of the fibers of the dorsal half of the muscle. These fibers lie proximal (anterior) to the ventral end of the ventral linear aponeurosis, and are inserted mostly on the bent-in ventral end of the ventral extrabranchial of the arch, but at the bend of that cartilage an important bundle crosses it, and passing ventro-posterior to the coracobranchialis of the second arch, and dorsal to the coracohyoideus, is inserted in fibrous tissues near the median line. At the proximal edge of the muscle, a superficial bundle of fibers separate from the underlying ones and is inserted on the ventral end of the ventral extrabranchial of the hyal arch.

The posterior efferent artery of the arch lies, as above stated, posterior to the branchial rays, and certain branches of it are sent outward along the posterior surface of the musculus interbranchialis, and others, which perforate that muscle, outward along its anterior surface. Certain of these branches reach the posterior (distal) edge of the muscle and there fall into the dorsal and ventral arteries that lie along the external, and hence anterior surfaces of the aponeuroses related to this muscle. The distal portions of these dorsal and ventral arteries thus apparently owe their origin to the anastomosis, with each other, of certain of the branches of these radial branches of the posterior efferent artery of the arch. Other branches of the efferent arteries anastomose with branches of the dorsal and ventral longitudinal commissures of the efferent arteries, and so form the basal portions of the dorsal and ventral arteries. The arterial loops that encircle the dorsal and ventral superficial bundles of the constrictor superficialis of the hyal arch would then be, in part at least, of glossopharyngeal origin.

The constrictor superficialis of the glossopharyngeus arch, the muscle Cs_3, is formed of those fibers of the primitive constrictor of the arch that were left after the interbranchialis had been cut out of it. The distal (posterior) fibers have a dorso-ventral course between the first and second gill openings, and are inserted, both dorsally and ventrally, on the linear aponeuroses related to the second gill opening. The more proximal (anterior) fibers, both dorsal and ventral, arise either from the aponeuroses related to the first gill opening, or from the underlying parts of the extrabranchials of this arch, the dorsal fibers running dorso-posteriorly, and the ventral ones postero-mesially, and most of them having their insertions on the aponeuroses related to the second gill opening. The most proximal (anterior) fibers of the dorsal half of the muscle

pass, because of the direction in which they run, dorso-anterior to the dorsal end of the aponeurosis related to the second gill opening, and, as already stated, they unite with the overlying superficial bundle of Csd_2 to form a muscle bundle which becomes tendinous and perforates the ventral edge of the trapezius to acquire insertion in the fascia that covers the trunk muscles. These fibers of the muscle Cs_3 thus correspond to that bundle of the muscle Cs_2 that passes dorso-anterior to the dorsal end of the aponeurosis related to the first gill opening and has its insertion beneath the anterior end of the ventro-anterior edge of the trapezius. Immediately distal (posterior) to this bundle of the muscle Cs_3, a bundle of superficial fibers separates from the deeper ones, passes external to the aponeurosis related to the second gill opening, internal to the related vein and through a loop of the related artery, and, uniting with the underlying fibers of the muscle Csd_4, perforates the ventral edge of the trapezius and acquires insertion in the fascia that covers the trunk muscles; this bundle thus corresponding strictly to the dorsal superficial bundle of the muscle Cs_2. In the ventral half of Cs_3, the origins and insertions of the fibers are strictly similar to those in the dorsal half of the muscle, but the proximal fibers are not gathered into muscle heads, persisting as a sheet-like muscle which is inserted in fibrous tissues along the lateral edge of the musculus coracoarcualis.

The interbranchialis and constrictor superficialis of this arch are both innervated, in all their parts, by branches of the nervus glossopharyngeus which run outward along the anterior surface of the interbranchialis, traverse the related linear aponeurosis, there passing internal both to the related vein and the dorso-ventral arteries, and then run posteriorly along the external surface of the constrictor superficialis. No branches of this nerve could be found going to the overlapping superficial bundles of the constrictor of the hyal arch, those bundles being supplied only by branches of the nervus facialis.

In the first vagus (second branchial) arch there are interbranchialis and constrictor superficialis muscles strictly comparable to those in the glossopharyngeus arch. In the ventral half of the muscle there are certain isolated bundles of the constrictor superficialis which run posteriorly external to the aponeuroses related to both the third and fourth gill openings and have their insertions on the shoulder-girdle along with the fibers of the muscle Cs_6. In the second vagus (third branchial) arch the conditions are also similar, excepting that in this arch, in the two specimens examined, no dorsal fibers of the constrictor superficialis separated from the deeper ones to form the superficial bundles found in the anterior arches. There was, nevertheless, in the related dorso-ventral artery, a loop strictly similar to those that, in the more anterior arches, enclose the superficial bundles.

In the third vagus (fourth branchial) arch, the interbranchialis does not differ from those in the more anterior arches, nor does the constrictor superficialis, excepting in the manner of its insertion. There is no aponeurotic line related to the fifth gill opening, that line being replaced by tissues that line

the anterior edge of the shoulder-girdle, and the fibers of the constrictor of this arch are in part inserted in that tissue but in large part traverse it and have their insertion on the posterior wall of the fifth gill-pouch. A dorsal bundle of the muscle forms a tendinous head and perforates the trapezius, as in the anterior arches, but is inserted on the internal surface of the shoulder-girdle instead of in the fascia related to the trunk muscles.

The conditions in the adult of this fish thus seem to show, quite conclusively, that the constrictor superficialis of a given arch primarily overlapped externally, to a certain extent, those of the next posterior arches, and that it retained its primitive innervation throughout its entire length. Later, these overlapping portions of the muscle were largely suppressed, remnants of them however persisting and being innervated by the nerve of their own arch, and not, as stated by earlier authors, by the nerves of the arches to which the underlying fibers belong. The suppression of the larger part of these overlapping fibers was probably largely due to their having become functionally supernumerary as soon as the linear aponeuroses related to the deeper muscle had become fully developed, for that deeper muscle was evidently primarily the more important one, and also lay nearer the source of its nerve supply. The efficiency of a given nerve must evidently have been impaired when it was crossed and somewhat pinched by an aponeurotic line, and while each nerve had, of necessity, to continue beyond the aponeurotic line that separates the interbranchialis and constrictor superficialis portions of the muscle of its own arch, that necessity did not exist at the second line, and the nerve and muscle accordingly both tended to abort beyond that point.

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DESCRIPTION OF PLATES

Plates XXIII—XXV

Fig. 1. Lateral view of the head of Acanthias Blainvillii, with the skin removed in the branchial region to show the veins enclosed in the subdermal tissue. $\times \frac{1}{2}$.

Fig. 2. The same with subdermal tissue and enclosed veins removed, showing the constrictores superficiales related to the branchial arches. One of the superficial bundles of these muscles cut and turned upwards. $\times \frac{1}{2}$.

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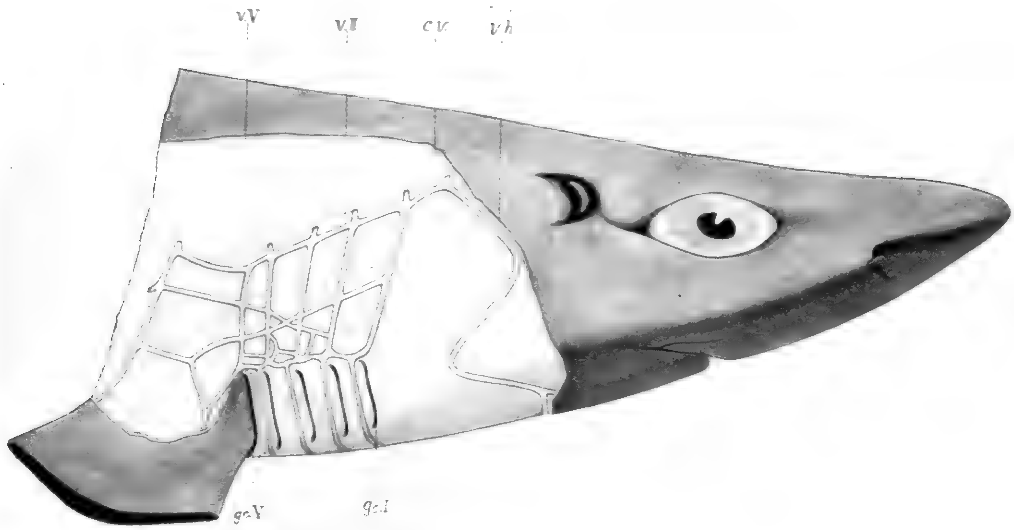

Fig. 1.

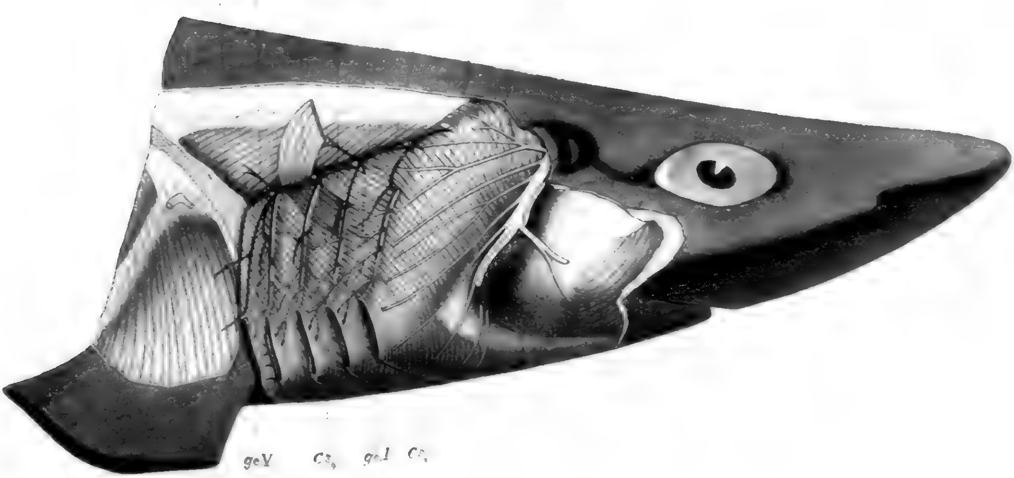

Fig. 2.

230[2]

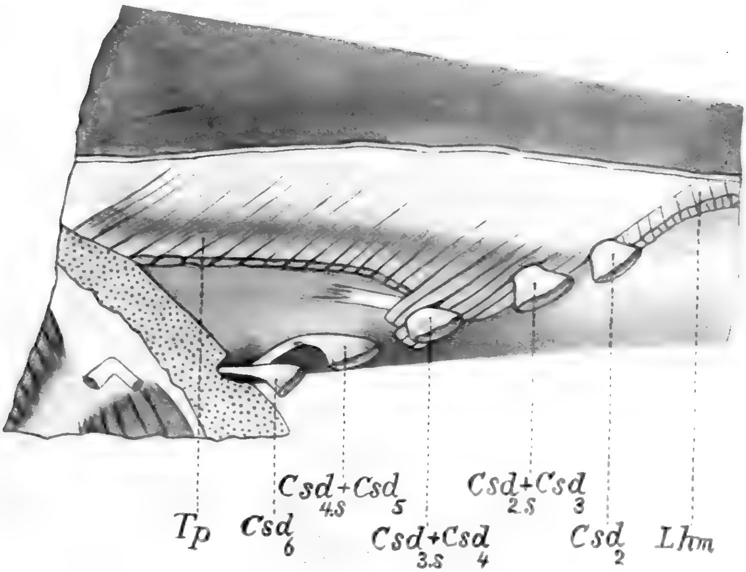

Fig. 3.

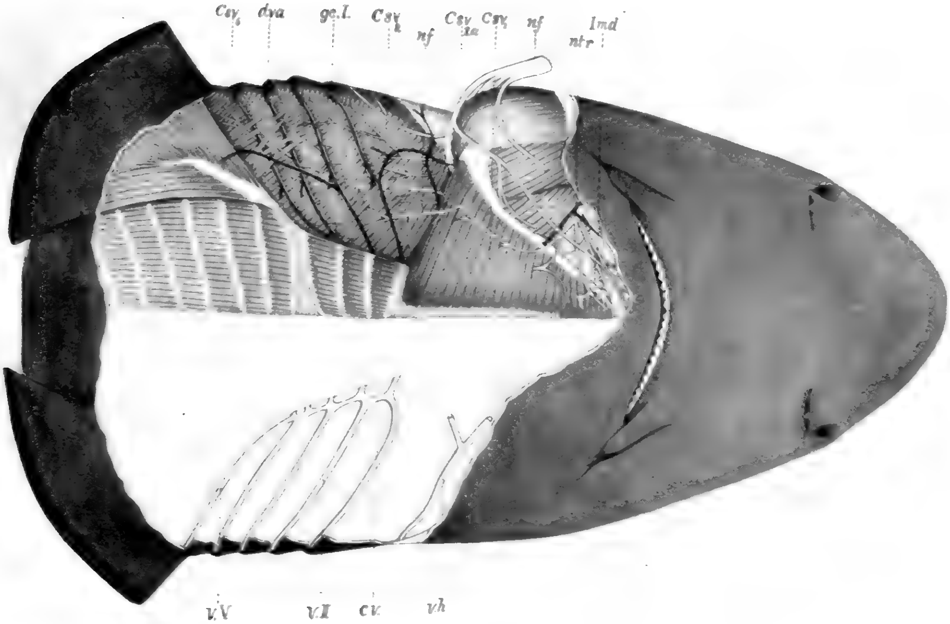

Fig. 4.

Fig. 3. Portion of the same showing the musculus trapezius and the insertions of the superficial bundles of the constrictores superficiales. $\times \frac{1}{2}$.

Fig. 4. Ventral view of the same, showing the veins related to the branchial arches on one side, and the constrictores superficiales and related nerves and arteries on the other. $\times \frac{1}{2}$.

Fig. 5. The same, the muscles Csv_1 and Csv_{2a} cut on one side of the figure and turned backward so as to show the underlying musculus interhyoideus. Parts of the constrictores superficiales cut and removed so as to expose the underlying extrabranchials. $\times \frac{1}{2}$.

Fig. 6. Antero-lateral vein of the musculus interbranchialis and constrictor superficialis of the first vagus arch. $\times 1\frac{1}{2}$.

INDEX LETTERS

BR ...	... Branchial ray.
Cs_{2-6}	... Mm. constrictores superficiales 2–6.
Csd_{2-6}	... Mm. constrictores superficiales dorsales 2–6.
$Csd_{2s} - Csd_{5s}$	Superficial bundles of Mm. constrictores superficiales dorsales 2–5.
$Csd_{2s} + Csd_3$	Superficial bundle of Csd_2, together with the underlying fibers of Csd_3.
$Csd_{3s} + Csd_4$	,, ,, Csd_3, ,, ,, ,, ,, ,, Csd_4.
$Csd_{4s} + Csd_5$	,, ,, Csd_4, ,, ,, ,, ,, ,, Csd_5.
Csv_{1-6}	... Mm. constrictores superficiales ventrales 1–6.
Csv_{2a}	... Ventral bundle of constrictor superficialis of hyoid arch.
cv ...	... Commissural veins connecting the dorso-ventral veins of the branchial arches.
dva ...	... Dorso-ventral arteries.
eaII	... Efferent branchial artery of the 2nd branchial arch.
EBR I–IV	Extrabranchial cartilages of branchial arches 1–4.
gc I–V	... Gill-clefts 1–5.
Ibr_4	... M. interbranchialis of 1st vagus arch.
Ihy ...	... M. interhyoideus.
Imd...	... M. intermandibularis.
Lhm	... M. levator hyomandibularis.
nf ...	... N. facialis.
ngl ...	... N. glossopharyngeus.
ntr ...	... N. trigeminus.
nv_1 ...	... 1st vagus nerve.
nv_2 ...	... 2nd vagus nerve.
Tp	... M. trapezius.
vh ...	... Dorso-ventral vein related to the hyoid arch.
v I–V	... Dorso-ventral veins related to the branchial arches 1–5.

THE TIBIA OF THE AUSTRALIAN ABORIGINE

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The tibia from the anthropological point of view is one of the most interesting of the long bones. Not only does it vary in length to a remarkable degree, but it presents numerous features which differ considerably in their degree of development in the primitive races as contrasted with the modern European. In addition, there is a distinct resemblance in many cases between the features of the tibia in primitive races and in the tibiae of prehistoric men. Naturally, under the circumstances, many observations have been made on the tibiae of various races with the result that material for comparison is generally abundant. The Australian tibiae, however, have not received any marked attention. So far as I have been able to discover, there is no systematic and complete anthropometric examination of the bone on record. In 1889 Arthur Thomson, in describing the appearances produced in the tibia by the attitude of squatting, referred to 14 Australian bones. Klaatsch of Breslau in 1910 noted the resemblance between the Australian tibia and that of Homo Aurignacensis. Apart from these and a few other references to isolated features, the tibiae of native Australians remain practically undescribed.

The account which follows is based upon the examination of the Australian tibiae in the collection of the Anatomical Museum of the University of Edinburgh. In all there are 236 tibiae in good condition. They were collected in various parts of Australia, but mainly in the Northern Territory by Dr W. Ramsay Smith, Permanent Head of the Department of Public Health of South Australia, whose enthusiastic devotion to science has never received any adequate acknowledgment, and they were presented by him to the University Anatomical Museum in order that they should be examined and described when the opportunity occurred.

GENERAL TECHNIQUE

The methods of examination are based on those recommended by Rudolf Martin in his *Lehrbuch der Anthropologie*. A short account will be given at the commencement of each section of the procedure adopted.

Length of the Tibia

Technique. Length of Tibia:—1. From the articular surface of the lateral condyle to the tip of the medial malleolus. This measurement was taken by Hepburn's Measuring Board.

1 *a*. Greatest Length of Tibia or Spino-Malleolar Length:—The distance from the tip of the intercondyloid eminence to the tip of the medial malleolus.

1 *b*. Length of the Tibia for comparison with the living:—Taken from the mid-point of the margin of the articular surface of the medial condyle to the tip of the medial malleolus.

2. Joint-surfaces distance:—The distance from the centre of the articular surface of the medial condyle to the least prominent point on the distal articular surface. It was obtained by means of the Parallelograph.

The average length of the 236 tibiae examined, measured from the articular surface of the lateral condyle to the tip of the medial malleolus, was 380 mm. The longest bone gave the remarkable figure of 446 mm. The shortest tibia in the series was 316 mm. in length.

In 2000 white American tibiae Martin found that the average length was 365 mm. in the male and 345 mm. in the female, or 355 mm. when the sexes are taken together. In other races the length varies from that of the short tibia of the Aino, which measures on the average only 331 mm. in the adult male, to that of the tibia of the Alamann, which reaches an average length of 373 mm. in the male and 342 mm. in the female, or 357·5 mm. when the sexes are taken together. It is evident, then, that the tibia of the Australian aborigine is longer than that of any other race yet investigated[1]. This fact becomes all the more remarkable when the other dimensions of the bone are examined.

The average spino-malleolar length was 386 mm., giving an increase of 6 mm. as the height of the intercondyloid eminence. References to the size of this process are very sparse in the literature. Klaatsch considers that a small intercondyloid eminence is a characteristic feature of the Orang-Aurignac type of tibia. I compared the size of the process in 20 European bones and found it in the latter to measure 5·1 mm., so that there is very little difference between the European bone and the Australian in this respect.

The length of the medial malleolus seems also to have received very little attention. Klaatsch lays stress on the great length of the malleolus in the Spy tibia and considers it of great importance as a feature of difference between the Spy tibia and the Aurignacian. In the Australian bones the average length was 13·8 mm., in a model of the Spy tibia in the University Anatomical Museum it was 19 mm., and in 118 Scottish tibiae measured in the Anatomical Department it was only 7·6 mm. The distinct difference in length of the process in the Australian and in the Scottish tibiae would seem to indicate that the length of the medial malleolus is worthy of more consideration for purposes of racial diagnosis than it has received.

The relation of the length of the tibia to the body-height is a factor which varies more than in the case of any other of the long bones. Topinard has published figures which prove this conclusively. Thus, in New Caledonians

[1] Martin's figures were published in 1914. I have not observed any larger figures in the literature since that date.

the proportionate length was 23·8, while in the Samoyede the tibia is only 20·8 per cent. of the body-height, a difference of 3 per cent. In females the extremes are even further apart, variations of as much as 4·2 per cent. having been described by Topinard. The tibia is, therefore, of comparatively little value in calculations of the body-height. In the present series complete skeletons were not available, but for the purpose of a rough estimation of the relationship, the body-heights which are given by Spencer and Gillen for natives of Central Australia were employed, these being the only figures at hand.

Spencer and Gillen found the average height of 30 aborigines to be 163·2 cm. If we take 380 mm. as the average length of the tibia, the relationship between length of tibia and body-height works out at 23·3. This is perhaps sufficient to indicate, when taken in conjunction with the comparisons of the measurements of length, that the Australian tibia is near the top of the scale when considered in relationship to body-height. The highest proportion described so far—as mentioned above—is the 23·8 of the New Caledonian.

Karl Pearson has worked out formulae by which the body-height may be calculated from the length of the various long bones. The formulae which he gives for the tibia are: $S = 78{\cdot}664 + 2{\cdot}376T$ for male bones and $S = 74{\cdot}774 + 2{\cdot}352T$ for female bones. In the Australian bones the sex is not stated in the majority of the specimens. If we presume, for purposes of a rough estimation, that there were equal numbers of male and female tibiae, the average living stature would work out at 166·55 cm., a little higher than the figure taken from Spencer and Gillen. If we take 166·55 cm. as the body-height the relationship of the tibia to the living stature works out at 22·8, still a ratio which is high in comparison with other races.

An asymmetry as regards the length of the two tibiae has long been recognised. In 93 pairs of bones from the present series, the two tibiae were equal in only 7·6 per cent. of cases; the right was the longer in 49·4 per cent., and the left in 43 per cent.

In concluding the consideration of measurements of length, it may be mentioned that, when the measurement was taken from the mid-point of the medial margin of the medial condyle to the tip of the medial malleolus, the average length was 377 mm. Therefore, when measurements are made in the living subject, it is necessary, at least in the Australian aborigine, to make an addition of 3 mm. so as to obtain the true length of the bone.

Dimensions of the Epiphyses

Technique. The epiphyses were measured in both the transverse and the sagittal directions. The Greatest Breadth of each was obtained by means of the Measuring Board. The Sagittal Diameter of the proximal epiphysis was measured at the level of the tubercle. That of the lower was taken as the distance between the anterior and posterior borders in the mid-line of the

bone and was measured always at right angles to the long axis of the shaft. In addition, the smallest transverse diameter of the proximal epiphysis at the level of the tubercle was taken. It was measured with callipers as the distance between the lateral and medial margins at that level. The sagittal measurements were also made with callipers.

The dimensions of the epiphyses of the tibia have not received in the past all the attention which they merit, but in the few instances in which they

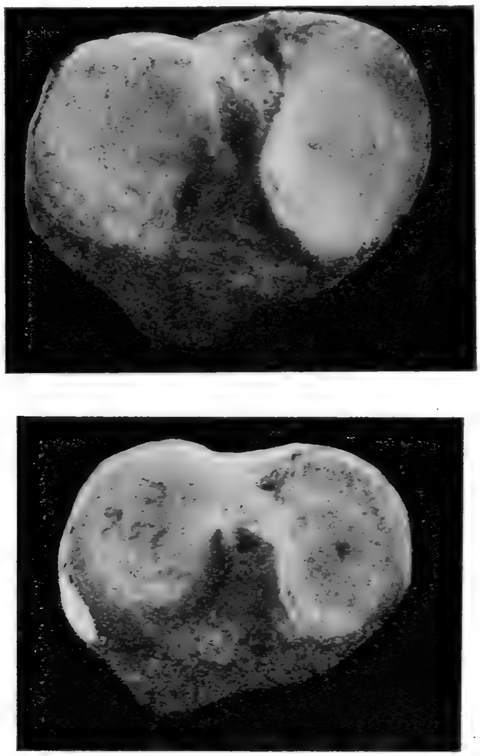

Fig. 1. The proximal aspects of a European and an Australian tibia of approximately the same length. The greater breadth and more massive character of the European epiphysis are clearly demonstrated. The two bones were photographed at the same distance from the camera.

have been carefully worked out, very pronounced race differences have been found to exist. If the breadth of the epiphyses alone is considered, very interesting results are obtained. In the present series, with an average length of 380 mm., the average breadth of the proximal epiphysis was 69 mm. and of the distal epiphysis 45 mm. For comparison with these figures and to illustrate the importance of measurements of epiphyses, the following table, which, with the exception of the Scottish and Spy measurements, is taken from Martin, is worthy of consideration.

	Length of tibia	Proximal epiphysis	Distal epiphysis
Swiss	365 mm.	72·7 mm.	51·7 mm.
Scottish	352 "	74 "	—
Fuegian	338 "	71·6 "	51·2 "
Aino	339 " male	73·7 " male	50·6 " male
	319 " female	67·4 " female	45·4 " female
Japanese... ...	333 " male	74·3 " male	50·8 " male
	309 " female	66·8 " female	45·4 " female
Spy	326 "	82 "	58 "
Senoi	323 " male	64 " male	43·5 " male
	319 " female	62·5 " female	40·5 " female

The Australian tibia is longer than any of the above and yet has the narrowest epiphyses except in the case of the very short tibia of the male Senoi, and in the females of the Senoi, Japanese, and Aino in whom the tibia is at least 60 mm. shorter. The huge epiphyses of the Spy tibia, the measurements of which are taken from a cast in the University Anatomical Museum, correspond to the thick clumsy diaphysis of that bone.

The sagittal diameters of the epiphyses correspond in a general way to the transverse. That of the proximal epiphysis in the Australian tibiae was 43 mm., that of the distal 34 mm. As similar measurements in other races were not available for comparison, I made the same measurements in 40 Scottish tibiae. The figures from these were 44·7 and 37·9.

Dimensions of the Diaphysis

Technique. The diaphysis was measured in the sagittal and the transverse diameters. The sagittal measurement was taken between the crest and the mid-point of the posterior surface by means of callipers:

(1) At the middle of the Spino-Malleolar length.

(2) At the level of the nutrient foramen.

(3) At the point where the popliteal line cuts the medial border.

The transverse diameter, *i.e.* the distance between the medial and interosseous borders, was measured at the same three levels.

The circumference of the diaphysis was measured by means of a narrow tape measure:

(1) At the middle of the bone.

(2) At the level of the nutrient foramen.

(3) The smallest circumference was estimated also, and was found to be situated usually in the distal third about the level at which the crest begins to disappear.

The average sagittal diameter at the three levels was (1) 2·9 cm., (2) 3·3 cm. and (3) 3·1 cm. The average transverse diameter at these levels was (1) 2 cm., (2) 2·2 cm., and (3) 2·1 cm. The average circumference at the three levels mentioned was (1) 8·1 cm., (2) 8·9 cm. and (3) 7 cm.

To indicate the relationship of the thickness of the tibia to its length, it is customary to employ the following index:

$$\frac{\text{Smallest circumference of diaphysis} \times 100}{\text{Greatest length}}.$$

The average index in the Australian bones worked out at 18. In the majority of other races this index is about 20. The smallest index recorded appears to be that of the Negro, which is 19·8 (Martin). The tibia of Spy and Neanderthal forms a marked contrast in this respect to the Australian tibia, the index for the Spy tibia being 26·2 and for the Neanderthal tibia 24.

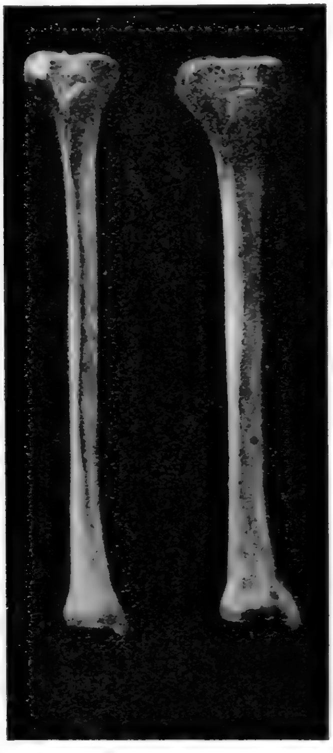

Fig. 2. A typical Australian tibia compared with a European bone of the same length. The Australian bone is more slender, both as regards the diaphysis and the epiphyses. Note the articular facets on the anterior aspect of the distal epiphysis and on the anterior border of the Australian specimen. The difference in the appearance of the area on the lateral condyle for the attachment of the ilio-tibial tract is well brought out.

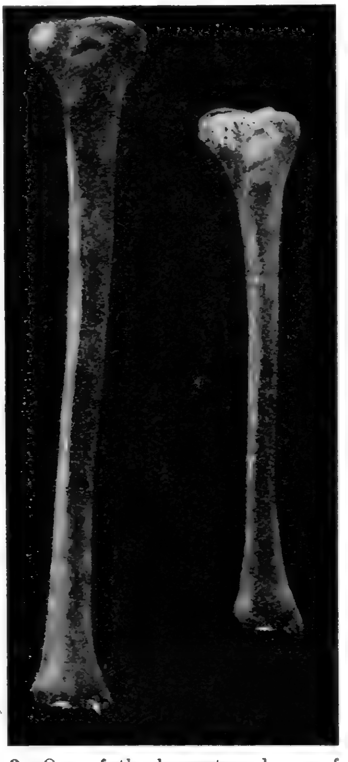

Fig. 3. One of the longest and one of the shortest of the Australian specimens. These were photographed at the same distance from the camera as the bones in Fig. 2.

It may be mentioned here that, as Klaatsch has noticed in the *Zeitschrift für Ethnologie*, the Australian tibia shows many points of resemblance to the Aurignacian tibia, especially with regard to the slender character of the diaphysis and the epiphyses, and differs widely in many respects from the Spy and Neanderthal bones.

From the measurements recorded so far it will be seen that the shape of the Australian tibia is quite characteristic. It is an extraordinarily long and slender bone with small epiphyses, differing distinctly in these features from the tibia of any other race which has been investigated. A typical specimen is illustrated in Fig. 2.

Platycnemia

For estimation of the degree of platycnemia in the tibia, the formula which is most commonly employed is

$$\frac{\text{Transverse diameter at level of nutrient foramen} \times 100}{\text{Sagittal diameter at same level}}.$$

Hrdlicka has objected that these measurements are affected by the degree of development of the linea poplitea and by variations in level of the nutrient foramen, and recommends that they should be taken instead at the middle of the bone. Accordingly, the measurements were taken, in the present investigation, not only at the level of the nutrient foramen, but also in the middle of the bone and at the point where the linea poplitea cuts the medial border, a third point which is recommended by some observers. It may be stated at once that the first level—*i.e.* at the nutrient foramen—which has been adhered to by Manouvrier, Broca and others, was found to be the most satisfactory of the three. The measurements at the middle of the bone and at the junction of the linea poplitea and the medial border fail to indicate the true degree of platycnemia since, in the majority of cases, they lie below the level at which the modification in shape of the tibia is well marked. Thus, the average index of the Australian bones at the level of the nutrient foramen was 65·2, at the middle 68·7, and at the junction of linea poplitea and medial border 67·7. These figures show clearly that to demonstrate the full degree of platycnemia the measurements should be taken at the level of the nutrient foramen, the level which gives the lowest cnemic index. It should be mentioned also that the third level—at the junction of linea poplitea and medial border—was found to be by no means constant, whereas the degree of development of the linea poplitea and the level of the nutrient foramen were not found to vary to any serious extent.

Manouvrier, in his classical work on platycnemia, adopted the following grouping when considering the cnemic index:

Index below 54·9	... ...	hyperplatycnemic
,, between 55 and 62·9	...	platycnemic
,, ,, 63 and 69·9	...	mesocnemic
,, over 70	... ...	eurycnemic

The average European tibia, which on section resembles an equilateral triangle, has an index of about 70. In bones with a lower index, the tibia appears to be somewhat flattened from side to side, having the appearance on section of an isosceles or a scalene triangle. The average index of the Australian bones was 65·2. The highest index was 86·2 and the lowest 50.

Of the total number of bones, only 7 were hyperplatycnemic, 74 were platycnemic, 114 were mesocnemic, and 41 were eurycnemic. The degree of platycnemia in the Australian aborigine may therefore be described as moderate. It corresponds to what is met with in such races as Polynesians, Andaman Islanders, American Indians, and Malays. The most marked degree of platycnemia is met with in the Aino whose index is 59·3 (Koganei). The index for the Cro-Magnon tibia is 64·5, while that for the Spy tibia is 85·8 and for the Neanderthal bone 71·3.

Manouvrier was the first to point out that the apparent flattening of platycnemic bones has for its object the provision of a larger surface of origin for the tibialis posterior, and that the essential cause of the peculiar shape of the tibia is a hypertrophy of that muscle. The hypertrophy in man is mainly due to the indirect action of the muscle, the action which comes into play when the foot is fixed on the ground and which immobilises the proximal end of the tibia so that it may support the weight of the body. This action is especially important when the knee is somewhat flexed, as in running or leaping. The resulting platycnemia is therefore more marked in races who live in rocky uneven country and who follow the chase. It is naturally absent in children and comparatively slight in women. Havelock Charles has shown that hypertrophy of the tibialis posterior and platycnemia are produced also by the attitude of squatting in races like the Punjabis who live on a level plain and who are not exposed to the factors above mentioned. The condition is also met with in modern European tibiae and in these is most likely due to occupations such as that of a hill-shepherd, where the cause is the same as in savage races, or that of a miner, where the prolonged adoption of a squatting attitude will act in the same way as in the Punjabis.

The explanation of Manouvrier has been criticised especially by Hirsch and by Klaatsch. Hirsch attempted to explain the condition of platycnemia by purely mechanical influences. He considered it to be an adaptation in the shape of the bone to resist forces which tend to bend it in a sagittal direction, such forces coming into play especially in running or jumping when the knee is flexed. He denied absolutely the influence of muscles on the external shape of the bone. The theory of Hirsch has already been completely refuted by the work of Fick, Guérin, Vallois, and others, and does not require further discussion.

Klaatsch objected to the theory of Manouvrier on the ground that it does not explain the absence of platycnemia in the Spy tibia, which was certainly exposed to the conditions producing platycnemia, and stated also that the essential change in platycnemia is not an increase in the antero-posterior diameter owing to the increase in the area of origin of the tibialis posterior but is, in reality, a diminution in the transverse diameter of the bone. Manouvrier explains the absence of platycnemia in the Spy tibia as the result of the remarkable shortness and thickness of the bone. The tibialis posterior already had a sufficient area of origin and no further increase in

the sagittal diameter of the tibia was required. The statement with regard to the relationship of the sagittal and transverse measurements has been made also by Derry. Derry founded his statement on the examination of between four and five hundred predynastic Egyptian tibiae. Unfortunately, he gives almost no measurements, having apparently merely inspected the bones, therefore the value of his conclusions cannot be properly estimated.

The examination of the Australian tibiae supported Manouvrier's views in every respect. They show that the principal change in platycnemia is not a simple transverse flattening of the bone, as Klaatsch and Derry have asserted. Manouvrier himself showed that the weight of platycnemic bones is equal to that of eurycnemic. The average transverse diameter of the Australian bones at the level of the nutrient foramen was 22 mm. In a considerable number of the platycnemic specimens the transverse diameter was actually above this figure, so that the factor which caused a lowering of the cnemic index was an increase in the sagittal diameter alone. The average sagittal diameter of the specimens with an index below 70 was 35 mm., while in those with an index of 70 or over the average sagittal diameter was only 32 mm., which shows clearly enough that in tibiae with a tendency to platycnemia the sagittal diameter is actually increased and the change is not due merely to a diminution in the transverse diameter.

Mere inspection of the area of origin of the tibialis posterior in the platycnemic bones showed that this area was much larger than in eurycnemic. To demonstrate the increase I measured the breadth of the origins of the tibialis anterior and posterior at the level of the nutrient foramen in the platycnemic specimens and contrasted them with similar measurements in 12 eurycnemic European tibiae. In the platycnemic bones the figure for the tibialis anterior was 22·3 mm. and for the posterior 18·3 mm., a difference of 4 mm. In the eurycnemic bones the figures were 26 mm. and 14·7 mm., a difference of 11·3 mm. These figures show that the tibialis posterior has a much bigger area of origin relatively to the tibialis anterior in platycnemic bones than in eurycnemic. The measurements given and the appearances of the muscular impressions on the platycnemic bones of Australian aborigines afford strong confirmation of Manouvrier's explanation of the cause of platycnemia.

The Outline of the Tibia at the Level of the Nutrient Foramen

Technique. With the tibia clamped in the vertical position a tracing of its shape on transverse section was obtained by means of the Perigraph.

Hrdlicka has made a special study of the outline of the tibia. He subdivided tibiae into six types according to their shape on transverse section. In the Australian bones five of Hrdlicka's types were represented. It was possible to obtain a tracing from 226 specimens only, the remainder being rejected on account of mutilations. An inspection of the tracings showed

that six groups could be defined and tracings illustrating the six varieties of outline are shown in Fig. 4.

No. 1 shows an outline which corresponds more or less to an equilateral triangle and therefore to the usual outline of a European tibia. Of this variety there were only 17 examples. No. 2 shows a rare form of tibia in which the lateral surface is distinctly hollowed out, probably to afford a larger area of origin to a powerful tibialis anterior. Only four examples of this type occurred. No. 3 was much the most common variety and 160 of the tibiae could be allotted to this group. The special feature of this group is the sub-

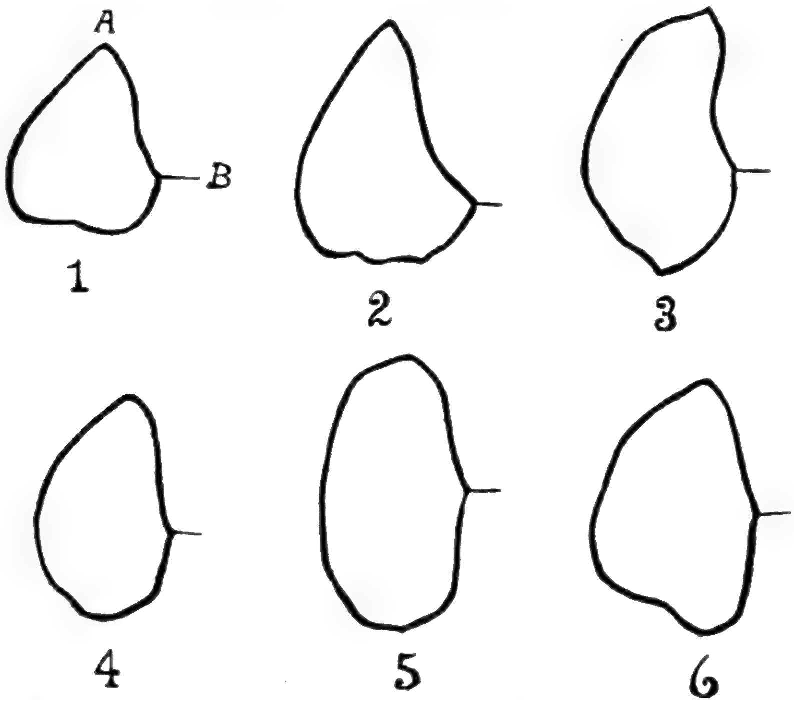

Fig. 4. The six types of outline occurring in the Australian tibiae. In No. 1, A = Anterior border, B = Interosseous membrane.

division of the posterior aspect into a postero-medial and a postero-lateral surface. It was shown by Manouvrier that this change in the outline of the tibia is due to a powerful development of the tibialis posterior and is the appearance usually found in platycnemic bones. No. 4 shows an outline in which the medial border is rounded off and the whole posterior half of the outline is more or less uniformly convex. Hrdlicka states that this variety of outline is practically limited to female tibiae. Twenty-seven of the tracings belonged to this group. The bones from which they were taken were mostly small and slender and probably of the female sex, supporting Hrdlicka's

observation. The fifth tracing shows a more or less oval outline, and of this type there were only eight examples. Hrdlicka states that this form is associated with marked platycnemia, that it is rare in Europeans and North American Indians but common in Negroes. The average cnemic index for the eight Australian bones was 58·4 which confirms the statement with regard to platycnemia. No. 6 illustrates a variety of tibia which is not included in Hrdlicka's types but which was described by Manouvrier. It shows that the origin of the tibialis posterior lies, in these bones, in the same plane as that of the tibialis anterior, while that of the flexor digitorum longus looks directly backwards. This form of tibia occurred in ten of the Australian bones.

Retroversion and Retroflexion

In the European the tibia is usually straight in its whole extent. By the term *Retroversion* is meant here the condition in which the diaphysis is straight

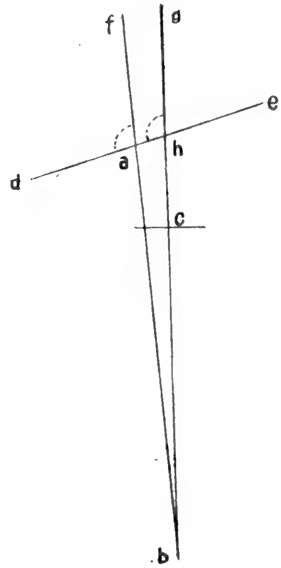

Fig. 5. *fad* = Inclination angle of the tibia. *ghd* = Angle of retroversion. *de* = Tangent to the superior medial articular surface, *a* is the mid-point of this surface, and *b* is the mid-point of the inferior articular surface. *baf* is the physiological axis. *c* is the mid-point of the lateral surface 2 cm. below the tubercle and *bcg* is the morphological axis of the tibia.

in its whole length but the proximal extremity is tilted slightly backwards. This retroversion of the proximal extremity is best expressed by the angle between the tangent to the articular surface and the axis of the diaphysis—the *Angle of Retroversion.* It is of some importance also to consider the angle which is formed by the same tangent and the physiological axis of the bone, the physiological axis being indicated by a line between the mid-points of the articular surface of the medial condyle and of the inferior articular surface. This second angle differs slightly from the first and is known as the *Angle of Inclination.*

By the term *Retroflexion* is meant a rather uncommon condition in which

the upper half of the diaphysis is distinctly bent backwards so that a pronounced posterior concavity of the bone results.

Technique. In measuring the angles of retroversion and inclination, the tangent to the superior medial articular surface was obtained by fixing a slender steel rod over the middle of the articular surface by means of a little putty. The bone was clamped in a horizontal position with the lateral surface upwards, in such a way that the steel needle was parallel to the marble slab underneath. The physiological axis was easily obtained from the mid-points of the articular surfaces by means of the parallelograph. A difficulty arose with regard to the morphological axis. Martin recommends a line drawn through two points, one of which is the mid-point of the inferior articular surface and the other the mid-point of the lateral surface 1 or 2 cm. below the tubercle. The boundaries of the lateral surface are the anterior border and the interosseous crest, so that the mid-point of the lateral surface should lie mid-way between these. But in many bones, and especially in those which are platycnemic, the interosseous crest curves very distinctly forwards towards its upper end. The result is that the lateral surface is considerably narrowed towards its upper end and the mid-point is carried further forwards than it would be in bones in which the interosseous crest is straight in its whole length. In tibiae with such a curvature at the upper end of the interosseous crest the axis of the diaphysis, marked in the manner indicated above, is inclined slightly forwards at its proximal end and the angle of retroversion is made to appear a little greater than it really is. After a consideration of various methods, including the method employed by Manouvrier, I decided that the method recommended by Martin was the least liable to error and I have adhered to that procedure throughout the investigation.

Retroversion was first described by Collignon in 1880. He attributed it to an attitude of incomplete extension of the knee-joint and regarded it as a legacy from a simian ancestor. Manouvrier showed conclusively, however, that retroversion is not only not inconsistent with the erect attitude but is actually an advantage in the extended position of the joint, especially in the Spy and other prehistoric forms in whom the lumbar curvature was presumably less developed than it is in modern races. He then set himself to formulate a fresh explanation for the existence of this character. He believed that it was due to the method of walking with the knee *en flexion* by the inhabitants of hilly countries. These people find that the least fatiguing method of walking over hilly and irregular country is to walk with the knees slightly flexed. The gait is well seen in hill-shepherds in this country. The arguments brought forward in proof of this theory are very convincing, but the work of Havelock Charles has shown than another explanation is the true one. He demonstrated the change in a well-marked degree in the tibiae of Punjabis who live in a plain as flat as Holland and whose gait is as erect as that of a Guardsman. He believed that the retroversion was due to the habit of extreme flexion of the joint in the act of squatting, acting from the earliest

childhood. The ligamentum patellae is attached to the diaphysis. In complete flexion of the joint the tension of the ligament on the anterior aspect of the epiphysis will have a tendency to bend it backwards. He showed that the squatting posture, which is adopted by natives of Eastern and savage races during many hours of the day, both at work and during leisure, has a profound effect on the conformation of the tibia.

Charles showed also that retroversion was present in the Punjabi infant and regarded it as a character inherited from ancestors in whom it had persisted or been acquired as the result of the squatting attitude. The association with the retroversion of the foetus of other features which result from the squatting attitude, namely, additional facets for the talus and convexity of the lateral condyle, favours this conclusion. G. Retzius showed that retroversion is present also in the foetus and child of modern European races. The change is most marked about the sixth month and rather diminishes towards the end of pregnancy. By the end of the first year of life the condition has almost disappeared in the European child. Hultkrantz explains the disappearance of the retroversion in the infant by the enforced extended position in which it lies. Retzius believes that this condition in European infants is a reminiscence of the earlier stages of their history and not simply the result of mechanical conditions during intra-uterine life, as has been suggested by Hueter. Klaatsch agrees with the opinion of Retzius.

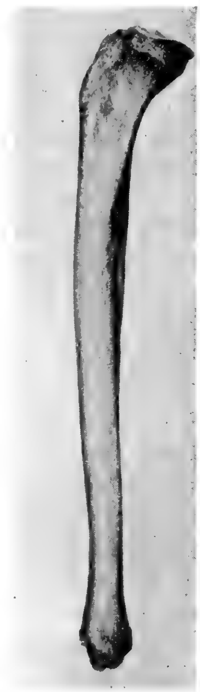

Fig. 6. A well-marked example of retroversion in an Australian tibia.

I found well-marked retroversion in the tibiae of one or two Australian infants which I was able to examine. In the 236 adult bones the average Angle of Retroversion was 17° and the average Angle of Inclination 13°, which form a marked contrast to the angles of about 7° and 5° which are usually found in modern Europeans. In comparison with other modern savage races the Australian angles are very high. The only races having a greater degree of retroversion are the Fuegians and the Californians, the retroversion angle in both of these being 20° and the inclination angle in the former being 16·5° and in the latter 15°. It seemed of importance, then, to discover if, in a race with such a well-marked degree of retroversion, the habitual attitudes correspond to that which is suggested by Charles as the cause of the condition. In the works of Spencer and Gillen on the Native Tribes of Central and Northern Australia there are numerous photographs illustrating the postures which the aborigines commonly adopt when in repose. The attitude of squatting, which is common to the majority of savage races, is sometimes adopted, as is also the "sartorial" or tailor position, but the most

common posture differs from these and is very characteristic. The position is illustrated in Figs. 7 and 8. The individual sits with the knees acutely

Fig. 7. In the central figure in this photograph the position of the foot in the common resting attitude can be seen. It is turned under the buttock in such a way that the buttock rests on its medial border.

Fig. 8. Another photograph illustrating the attitude of exaggerated genuflexion which is the common posture of rest in the Australian aborigines. Both photographs are reproduced from the works of Spencer and Gillen by permission of Macmillan and Co.

flexed and directed straight forwards. The thigh is in contact with the calf and the weight of the body is transmitted through the thighs to the back of the leg and thence to the ground through the whole length of the leg proper

and through the feet. The position of the feet varies. In the majority of cases they are placed underneath the buttocks at a right angle to the leg and with the great toes directed towards each other or overlapping. The person actually sits on the medial borders (see Figs. 7 and 9) of the feet or even on the sole of the foot, the lateral borders or the dorsum of the foot resting on the ground (see Figs. 9 and 10). In other cases the buttocks rest on the heels and the foot

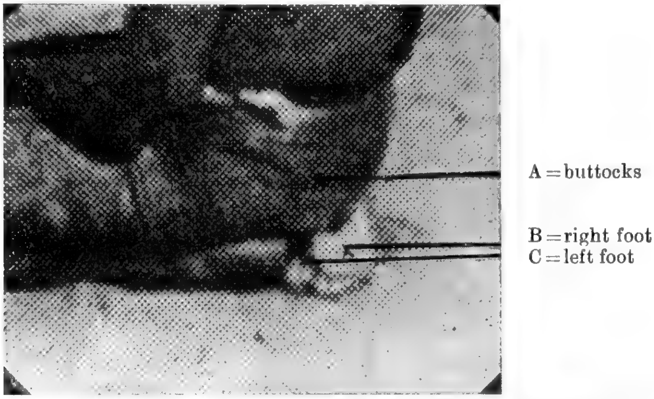

Fig. 9. This photograph shows both feet crossed under the buttocks, the weight of the body being transmitted to their medial borders. Enlarged from Spencer and Gillen by permission of Macmillan and Co.

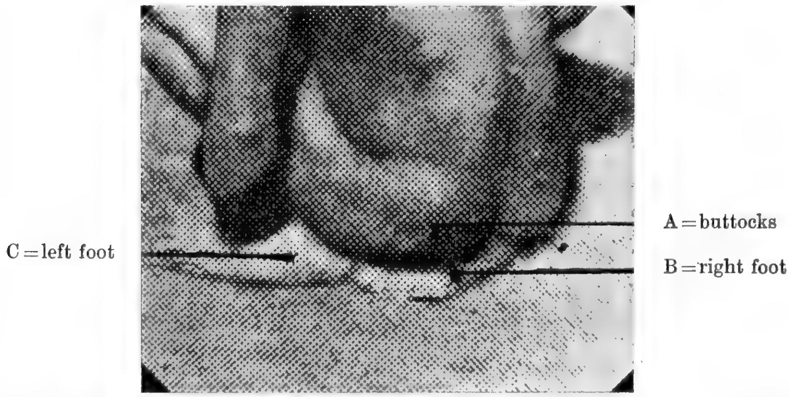

Fig. 10. In this photograph, which is from the same source as Fig. 9, it will be seen that the whole weight of the body is resting on the sole and medial border of the right foot. This demonstrates the remarkable degree of rotation of the foot which is possible in aborigines.

may be either acutely dorsiflexed at the ankle-joint or may be plantar-flexed so that the dorsum of the foot rests on the ground. It is interesting to notice that the attitude adopted by the females corresponds to that described by Dr St John Brooks and quoted by Arthur Thomson with reference to Zulu girls. They sit with the buttocks and one thigh on the ground, with the knees flexed, and the legs directed to the opposite side. Occasionally the

females take up the position of extreme genuflexion which is the common resting position of the males. It is obvious that in these positions there is the same tension on the ligamentum patellae as in squatting and the effect on the position of the proximal epiphysis is the same.

Retroflexion. Retroflexion of the tibia is a change which has received comparatively little attention. Manouvrier pointed out that the proximal extremity lies normally behind the prolongation of the axis of the diaphysis and that there is therefore a constant tendency to backward bending of the diaphysis. This tendency will be greatest when the tibia is inclined forwards, as in running downhill or leaping. The tibia in certain subjects is unable to resist the strain and a certain amount of bending of the diaphysis takes place. He found that the change occurred most commonly in platycnemic races and that the individuals presenting it were usually robust and muscular.

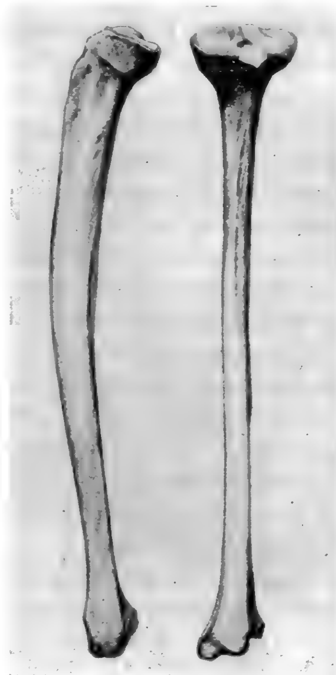

Fig. 11. An example of retroflexion in an Australian tibia.

Klaatsch emphasises the importance of distinguishing between retroversion and retroflexion. He believes that the two changes are dependent on different states of erectness of the tibia. He noticed in European tibiae a slight concavity of the anterior border, the starting-point of the concavity being at the same level as the commencement of the backward bend in a retroflexed bone. He found retroflexion especially marked in the Veddah tibia. He suggests that races presenting this feature may represent an intermediate stage between the race of Spy and the modern European or, on the other hand, that the European tibia may represent a line of development in one direction and the retroflexed tibia development in another, both having originated from the same starting-point. The common ancestral form is presumed to have resembled the Spy tibia, which is not so strongly retroflexed as the Veddah, but much more so than the modern European tibia.

To verify the observation of Klaatsch I examined a series of 118 European tibiae and found in the majority of cases the appearance he described. In most bones it was not so much a concavity of the anterior border as a gradual slope upwards and forwards to the tubercle. In the Australian tibiae retroflexion was not common. It was present in only 31 of the 236 specimens and in only 9 was it well marked. The curve in the majority of cases commenced at the junction of the proximal and middle thirds of the diaphysis. I was

able to verify the observation of Manouvrier that retroflexed bones are robust and show well-marked muscular impressions. The average cnemic index for the 31 retroflexed specimens was 64·9, so that a marked degree of platycnemia was not present. Indeed, four of the bones had an index of over 70.

Convexity of the Articular Surface of the Lateral Condyle

In modern European tibiae the surface of the lateral condyle is often very gently convex from before backwards. In savage races, as was first pointed out by Arthur Thomson, this convexity is very much greater. He attributed it to the habitual adoption of the attitude of squatting. He pointed out that in flexion of the knee-joint the lateral meniscus moves backwards to a certain extent. In the extreme flexion associated with the squatting position this backward movement is much facilitated by an increased convexity of the articular surface of the lateral condyle. Thomson made his observations by moulding a strip of soft lead across the centre of the articular surface of the lateral condyle in the antero-posterior direction. From this he was able to make a tracing. He then arranged the tracings into five groups according to the degree of curvature which they displayed. In the present investigation I was able to obtain tracings from 218 bones with the Perigraph, an easier and more accurate method.

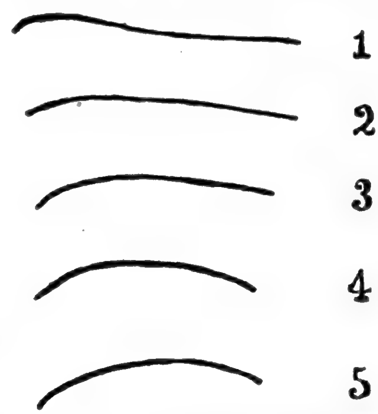

Fig. 12. A reproduction of Thomson's tracings illustrating the varying degrees of convexity of the articular surface of the lateral condyle.

The average curve in the present series corresponded to 2·3 of Thomson's scale, the figure which he himself gave for Australian tibiae being 2·5. A few bones showed as much curvature as his fourth type. In other races the average curvature varies from 1·5 in the European to 3·2 in the North American Indian. A curvature of 2·5 to 2·7 is common in many modern savage races. Although the explanation of Thomson as to the cause of the curvature is undoubtedly correct in the majority of cases, it may be pointed out that it is not the attitude of squatting alone that produces the condition. The curvature is well marked in the Australian but, as has been mentioned, the common attitude of rest in this race is not that of squatting, but an exaggerated kneeling position. In this position extreme flexion of the knee is also present and acts in the same way on the proximal end of the tibia.

A tracing taken transversely across the middle of the articular surface showed a gradual upward slope towards the intercondyloid eminence from about the centre of the condyle, a feature which, as was pointed out by Humphry, adds very considerably to the antero-posterior convexity of the

medial portion of the articular surface. The lateral part of the articular surface, as shown by this tracing, was practically flat.

There is no constant relationship between the degree of convexity and the degree of retroversion. The average angle of inclination from a series with a high convexity was much the same as that from a series with a low convexity. The same remark applies to the relationship to platycnemia. In a group of 25 tibiae in which the convexity was 3 in 22 cases and 4 in 3 cases, according to Thomson's scale, the cnemic index varied from 51·9 to 86·2, the latter being the highest index of the whole series. This last specimen with the high index had a convexity of 3. The average index for the group was 65·9 which differs very little from the average of 65·2 for the whole series. This bears out the generally accepted view that, though the convexity of the lateral condyle and platycnemia are commonly associated, they are dependent on essentially different causes, the former to habitual posture and the latter to hypertrophy of a muscle.

Articular Facets on the Anterior Margin of the Distal Epiphysis

In European tibiae the anterior margin of the distal epiphysis is usually sharp and well defined, but in most primitive races it presents an articular facet towards the fibular side. The facet is directly continuous with the distal articular surface. A similar facet will be found on the neck of the talus which fits exactly into the tibial facet when the two bones are articulated. Arthur Thomson, who first described this condition, attributed it to the extreme dorsiflexion at the ankle-joint in the act of squatting. Havelock Charles described also a second facet of a smaller size and occupying a more medial position. He found the medial facet present in 47 per cent. of Punjabis, while the lateral facet was present in 64 per cent.

In the Australian bones I found the lateral facet present in 190 out of the 236 bones (see Fig. 14). The medial facet was rarely present. It occurred alone only twice and in association with the lateral facet in three specimens. The difference in frequency in the occurrence of the medial facet in Australians and Punjabis is probably to be explained by the difference in the habitual attitudes of the two races. The lateral facet is sometimes found in European tibiae. In 118 European bones I found it in 20 specimens. The medial facet was present in two specimens. To explain these appearances in European bones Regnault has attempted to assign them to modifications in the shape of the articular surfaces. The work of Lane and others, however, has shown that they are much more likely to be due to factors which come into play as the result of the occupation of the individual. Heredity having determined the general shape of the bone, the development of the peculiarities in the adult bone is due to the assumption of attitudes at work, as in the occupation of a miner, which correspond very much with the squatting posture and are associated with marked dorsiflexion at the ankle-joint.

Variations in the shape of the *medial condyle* have been described by

different observers. Havelock Charles found that in Punjabis the articular surface is never horizontal in the transverse direction, as in Europeans, but slopes considerably downwards and medially from the intercondyloid eminence. He attributes this modification to the squatting position. I did not find this change present in the Australian bones, in which the articular surface was as horizontal as in the European. In view of the difference in the habitual attitudes of Punjabis and Australians, the absence of this variation is not surprising.

Martin makes the statement that in primitive races the medial condyle seems to lie relatively lower and more inclined medially than in the European, owing to which the whole articular surface is sloping slightly from the lateral to the medial side. This appearance was not present in the Australian bones, and in several specimens the proximal epiphysis was slightly tilted in the opposite direction so that the medial condyle was at a slightly higher level than the lateral.

Torsion of the Tibia

Although torsion has long been recognised, it was not until comparatively recently that its importance, especially with regard to the origin of man, was fully understood. P. le Damany and Klaatsch deserve the greatest credit for the work they have done in connection with this feature. Le Damany showed that the condition is absent in infants and is mainly due to the habit, which we instinctively acquire, of turning the point of the foot laterally to improve the base of support when standing. By the fifth or sixth year the angle of torsion has attained approximately the value which it will have in the adult. He found also that in most cases the torsion is greater in the right tibia than in the left and pointed out that prehistoric tibiae are twisted like those of our contemporaries and to the same degree.

Klaatsch pointed out the significance of the fact that in the higher anthropoids the torsion of the tibia is in the opposite direction to that of man and the improbability of the positive angle of man having developed from the negative angle of the anthropoids.

Technique. To measure the angle of torsion, a steel rod was fixed transversely over the mid-points of the articular surfaces of the two condyles to indicate the transverse axis of the proximal epiphysis. The transverse axis of the distal epiphysis was indicated in a similar manner. The tibia was then clamped in the vertical position so that the two axes crossed as nearly as possible at the centre of the two epiphyses. The two axes were then easily marked on paper by the Parallelograph and the angle measured.

The angle of torsion is about 19° in modern Europeans. In the lower races it varies from 14° in the Japanese and 18° in the Negro to 23° in the Malay. The low degree of torsion in the Japanese is probably due to their manner of walking. In the Australian bones the average angle of torsion was 17°. This figure is next to the Japanese when compared with other modern races. In searching for an explanation of this low degree of torsion

I convinced myself by the examination of a large number of photographs from the works of Spencer and Gillen already referred to, that in standing the Australian aborigine turns his toes laterally to a lesser degree than the European. Another factor which probably tends to diminish the amount of torsion is the habit of resting in the kneeling position previously described, with the feet turned medially under the buttocks so that the toes point towards each other. Klaatsch makes the statement that Australian females stand with their feet practically parallel with the median sagittal plane of the body which is in conformity with the appearances depicted in the abovementioned photographs.

Le Damany made the observation that the angle of torsion was usually greater in the right tibia than in the left and suggested that the difference was connected with right-handedness. In the present series the reverse condition was present. In 86 pairs of tibiae the left angle was the greater in 70 cases, the right in 15, and the two angles were equal in only one pair of bones. On working out the average angle on the two sides I was much impressed by the marked difference; the average angle of the right tibiae in the 86 pairs was 12·6°, that of the left was 21·6°. Unless the Australians are left-handed, a point on which I have no information, I have no explanation to offer for this striking difference.

An Impression on the Anterior Aspect of the Lateral Condyle

While examining the Australian bones I was struck by a prominence on the anterior aspect of the lateral condyle. The prominence bears an ovoid or circular impression about 7 to 10 mm. in diameter, flattened or slightly concave, with a smooth surface of dense compact bone—almost having the appearance of an articular facet. The impression was almost constantly present; in 236 specimens it was absent or poorly marked in only 43 cases. On examining European tibiae I found a similar impression, which has been noticed by Professor Thomson, occasionally present. In 118 European bones it was distinctly present in 20 and faintly marked in other 8.

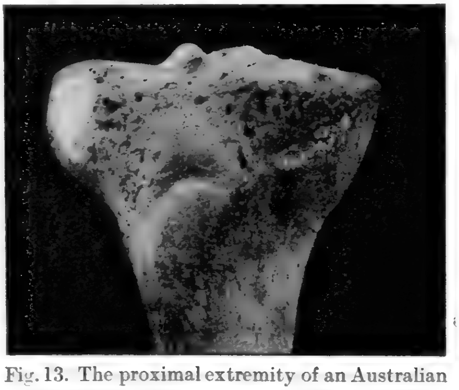

Fig. 13. The proximal extremity of an Australian tibia showing the facet on the lateral condyle.

The question arose as to whether this was a pressure facet or due to some other cause. The first idea that suggested itself was that it might be connected with the peculiar attitude of extreme genuflexion that the aborigines take up when resting. In this position one can quite easily demonstrate that there is a considerable degree of pressure on the lateral

condyle, though the pressure is mainly borne on the tubercle of the tibia. Against this explanation is the fact, which an examination of pathological specimens at once reveals, that although adventitious facets are of common occurrence where two bony surfaces are in contact they practically never result from pressure applied to a bone through the skin. Examination of the skeleton of a foot from a case of talipes equino-varus in a man aet. 50 demonstrated this clearly. Although the man had walked on the lateral border of his foot for nearly 50 years, the bones presented no appearances like the one under discussion.

The other possibility that suggested itself was that the impression might be produced by the attachment of an anatomical structure. A similar smooth dense surface is produced by the ligamentum patellae where it is attached to the tubercle of the tibia, or, less typically, by the tendo calcaneus where it is attached to the calcaneus. The only structure attached in this neighbourhood likely to produce such an impression is the ilio-tibial tract. In European bones the tract is usually described as being attached to a horizontal ridge on the antero-lateral aspect of the lateral condyle. In order to verify this description I dissected the attachment of the ilio-tibial tract in six specimens. I found that the attachment extends forward from the tibiofibular joint on to the anterior aspect of the lateral condyle. It is closely blended below with the attachment of the capsule of the knee-joint though the two structures can be separated at a higher level. The anterior portion of the tract extends distally on to the anterior aspect of the condyle and is attached to the area under discussion. This anterior portion constituted the strongest part of the tract. In European bones the area of attachment gives the appearance of a flat triangular surface bounded in front by a faint elevation and below by the ridge indicating the line of attachment of the deep fascia of the leg. The surface of the bone in this area was rough and similar in appearance to the neighbouring parts.

Apparently in the Australian bones the facet is due to the attachment of an unusually well-developed ilio-tibial tract. It may be presumed that the active conditions of life which cause platycnemia will throw an increased strain on the tract and conduce to its powerful development. It will be of interest in future investigations to observe if this appearance is present in other primitive races.

Some Minor Points in connection with the Distal Epiphysis

Martin has referred to variations in the general shape of the distal epiphysis in connection with the tibia of the natives of Tierra del Fuego. He found the distal epiphysis more flattened from before backwards than in Europeans; the anterior aspect was slightly concave while the posterior surface was strikingly flat, with no indication of a groove for the tendon of the tibialis posterior. In the Australian bones, apart from the generally slender character of the epiphysis, there was no striking difference in shape

A

B

C

Fig. 14. *A* is the distal extremity of a European tibia, *B* and *C* are the extremities of Australian bones. The articular surface of the medial malleolus terminates in the European bone in a sharp anterior border, in the Australian specimens it is continued on to the anterior aspect of the malleolus. Note also the facet on the anterior border of the distal extremity in the Australian bones.

Transverse diameter of $A = 5{\cdot}2$ cm.
" " " $B = 4{\cdot}5$ cm.
" " " $C = 4{\cdot}15$ cm.

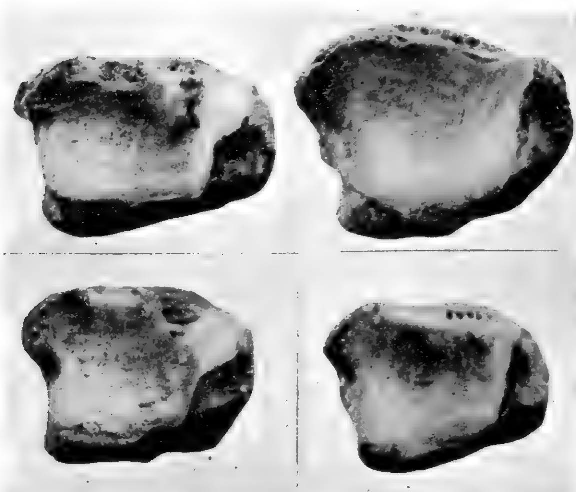

Fig. 15. The same appearances as in Fig. 14 demonstrated by photographing the distal articular surface. The two bones on the left are Australian and the two on the right European.

from the epiphysis of the European tibia. The anterior aspect was gently convex and the groove for the tibialis posterior was, as a rule, well marked.

The medial malleolus, however, showed in many cases a distinct difference from that of the European bone. As has been already mentioned, its average length is almost double that of the European malleolus, and it shows a more distinctly conical shape. When looked at from the front, the malleolus frequently presented an appearance which I have not seen described in the literature. The anterior border was somewhat everted or bevelled, so that there was an extension of the articular surface on to the anterior aspect. This additional articular facet is illustrated in Figs. 14 and 15.

It varied in the degree of its development in different cases but was well marked in 26 specimens. In other bones, in which there was no facet on the anterior border of the malleolus, the malleolus was markedly oblique, the whole process being bent in the medial direction. Both of these changes are probably related to the attitude of the foot in the positions of rest. The foot of the Australian aborigine seems to have an extraordinary degree of

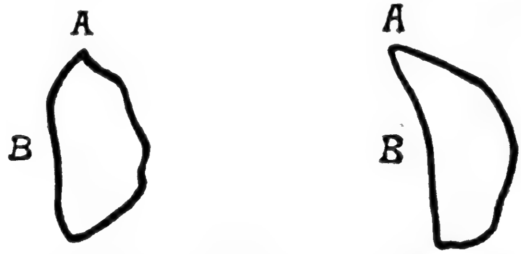

Fig. 16. Tracings taken in the transverse direction at the mid-point of the medial malleolus in an Australian and a European tibia. In the European bone—on the right—the articular surface B is slightly concave and terminates in front in a sharp border A. In the Australian specimen the anterior border of the articular surface is rounded off so that it extends on to the anterior aspect of the malleolus.

mobility at the ankle-joint, and the resting position in which the lateral border of the foot is placed on the ground and the toes are turned medially—which has been referred to repeatedly—would tend to bring the talus into firm contact with the malleolus. In some cases, as a result of the strain on the malleolus, the whole process becomes bent medially, while in others the anterior border of the malleolus becomes bevelled off so as to permit the talus to be slightly rotated in the medial direction around a vertical axis.

Klaatsch describes a feature on the distal epiphysis which he calls the Praefibular Process. This consists of a prolongation of the anterior border of the incisura fibularis so as to form a somewhat peg-shaped process. The articular surface extends on to the lateral aspect of the process, the articular area on this projection being separated from the rest by a definite border. He found it especially well marked in the Australian tibia. Examination of the present series supported this observation, the process being commonly present and showing a very definite extension of the articular surface on to its lateral aspect.

Pathological Conditions illustrated in the Australian Tibiae

A review of all the Australian tibiae in the Anatomical Museum revealed very few examples of disease. Two specimens, however, showed undoubted evidence of arthritis deformans of the knee-joint. The most important factor in the causation of this disease in civilised races is generally regarded as an "auto-intoxication," in the form, in most cases, of absorption of a soluble toxin from the alimentary canal. That such a prolonged intoxication should take place in a race like the Australians, who lead an active life under natural conditions, is difficult to believe. It would therefore seem possible that certain types, at least, of the disease are dependent rather on an organismal infection of the affected joint or joints than on any prolonged derangement of metabolism.

One pair of bones showed signs of advanced syphilitic disease. A few specimens showed the presence of small sequestra in the diaphysis surrounded by an area of osteoporosis. These were most likely due to tuberculosis. Several specimens illustrated the condition which Stirling has termed "campocnemia." The bones affected by this condition are very long and are markedly curved with the convexity forwards. The diaphysis is considerably thickened and the bone shows a marked degree of torsion, usually to about half a right angle. The appearance of these bones suggests a resemblance to the condition known as Paget's disease or Osteitis deformans, or to a condition resembling rickets in the adult. It may be that the bones become softened and bent during a period of malnutrition, such as those to which a race like the Australian aborigines is continually being exposed, and are restored to their former rigidity when the bad time has passed, preserving the deformity which has developed during the period of malnutrition.

SUMMARY AND CONCLUSIONS

1. *Length of the Tibia.* The average length of the 236 tibiae examined, measured from the articular surface of the lateral condyle to the tip of the medial malleolus, was 380 mm. The longest tibia was 446 mm. and the shortest 316 mm. The average length is greater than in any other race yet investigated. The intercondyloid eminence is well-developed and slightly longer than in European tibiae. The medial malleolus is longer than in European tibiae but considerably shorter than that of the Spy tibia. The Australian tibia is very long in proportion to the average body-height. The tibiae of the two sides are nearly always asymmetrical as regards their length; they were equal in the present series in only 7·6 per cent. of cases, the right tibia being more often the longer of the two.

2. *Dimensions of the Epiphyses.* The slender character of the epiphyses of the Australian tibiae is very striking, especially when considered in relation to the great length of the bone. The average transverse diameter of the proximal epiphysis was 69 mm. and of the distal epiphysis 45 mm. The corresponding sagittal diameters were 43 mm. and 34 mm. These measure-

ments are much smaller than those recorded for any other race, with the exception of a few examples with very short tibiae.

3. *Dimensions of the Diaphysis.* The average sagittal diameter at the middle of the tibia was 2·9 cm.; at the level of the nutrient foramen it was 3·3 cm.; and at the point where the popliteal line cuts the medial border, it was 3·1 cm. The average transverse diameter at these levels was 2 cm., 2·2 cm., and 2·1 cm. The average circumference at the middle of the bone was 8·1 cm.; at the level of the nutrient foramen it was 8·9 cm.; the smallest circumference was 7 cm. The Index of Massiveness or relation of thickness to length is lower than in any other race on record.

4. *Platycnemia.* The average cnemic index for the series was 65·2. The Australian tibia therefore occupies an intermediate position in this respect when compared with that of other races. Examination of the specimens with well-marked platycnemia confirmed in every respect the view that the essential cause of the change is hypertrophy of the tibialis posterior.

5. *Outline of the Tibia at the Level of the Nutrient Foramen.* The most common appearance of a transverse section of the Australian tibia is that in which the posterior aspect is subdivided into a postero-lateral area for the tibialis posterior and a postero-medial area for the flexor digitorum longus. A type of platycnemia in which the surface for the tibialis posterior lies in the same plane as that for the tibialis anterior, which is very rare in other races, occurred with comparative frequency.

6. *Retroversion and Retroflexion.* In the Australian tibia the average Angle of Retroversion was 17° and the average Angle of Inclination was 13°. These angles are very high in comparison with those of other races. The high degree of retroversion is due to the marked genuflexion in the common attitude of rest, and not merely to the attitude of squatting. Retroflexion is not of frequent occurrence in the Australian tibia. The bones in which it is present are strong and well-formed, so that it is probably not due to yielding of the bone to forces tending to bend it in the sagittal direction.

7. *Convexity of the Articular Surface of the Lateral Condyle.* The average degree of this change in the Australian tibia corresponds to 2·3 of Thomson's scale. Like retroversion it is due to habitual acute flexion of the knee-joint in the common attitudes of rest, which are not necessarily squatting attitudes. There is no constant relationship between the degree of convexity of the condyle and the degree of platycnemia.

8. *Articular Facets on the Anterior Border of the Distal Epiphysis.* The lateral facet is almost constantly present; the medial rarely occurs. These facets are due to habitual extreme dorsiflexion at the ankle-joint in the postures of rest.

9. *Torsion of the Tibia.* The average angle of torsion in the Australian tibia is 17°. This low figure probably depends partly on the method of walking and partly on the position of the feet in the common attitudes of rest. There is a very striking difference between the angles on the two sides, that on the

left being usually much greater than that on the right. This is the converse of what is found in most other races.

10. *An Impression on the Anterior Aspect of the Lateral Condyle.* The majority of Australian tibiae present a well-marked circular or ovoid smooth facet, flattened or slightly concave, on the anterior aspect of the lateral condyle. This is occasionally, but much less frequently, present in the European tibia. It is produced by the attachment of a powerfully developed Tractus Ilio-tibialis.

11. *Minor Points in Connection with the Distal Epiphysis.* The medial malleolus not infrequently shows an extension of the articular surface on to its anterior aspect. In other cases the medial malleolus is bent in the medial direction. These changes are probably due to the position of the foot in the common attitudes of rest. The Praefibular Process of Klaatsch is commonly present in the Australian tibia.

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MODELS OF THE HUMAN STOMACH SHOWING ITS FORM UNDER VARIOUS CONDITIONS

By A. E. BARCLAY, M.A., M.D. (Camb.)

With the advent of the opaque meal and X-ray method of examination of the alimentary tract, it at once became evident that the time-honoured diagrams and descriptions of the stomach were seriously at fault. There were many points, even in the gross anatomical appearances, which were incompatible with the shadows seen by means of X-rays. This was hardly to be wondered at, considering that the old descriptive anatomy was written from observations on post-mortem and preserved specimens, corrected to a certain extent by operative appearances, which, owing to the anaesthetic, the prone position and various other factors were hardly a true picture of the living functioning stomach. There is little to be gained by reviewing the literature on the subject, the fruitless discussions as to unnatural biloculations and the varied appearances of excised stomachs which were due to formalin or other factors. To-day I do not think that any anatomist will raise his voice in protest when a radiologist describes the stomach as "J" shaped, "cow's horn" shaped, or any other shape; for thought progresses, and it is realised that the radiologist sees the *living anatomy*, and it is for the radiologist, or those who have efficient X-ray installations at their disposal, to say what is and what is not the shape of the living stomach—the day of the description of dead specimens as essentially representing the conditions of life has gone for ever. As a radiologist who has examined well over 7000 living, functioning stomachs, I claim to speak with some authority, and yet, in spite of such an experience in the screen examination of both normal and pathological patients, it is with no little diffidence that I send forth these models as representing the normal stomach.

The essential fact in understanding the normal stomach is that one must think of it as a living muscle; that it is a sensitive organ, that it is perhaps the most sensitive muscular organ in the whole body.

In the early days of gastric work, one used to record atony of the stomach in one's notes as a pathological condition, till various object lessons taught one otherwise: for instance, a sudden dropping of the lower border was the first sign that a patient was going to faint. This was noted fairly frequently in the early days during the prolonged examinations that were necessary. The sudden banging of a door, or an unexpected touch by the screen on the patient's chin brought about the same result. Sometimes we recorded a marked atonic condition one day, only to find that it had gone when he came for re-examination and was less apprehensive. One could write at length on this subject, but my only object in mentioning it is to emphasise the point that in making models of the normal stomach I am doing something which is quite contrary

to nature, *i.e.* attempting, for teaching purposes, to give a standard picture of a living organ which may alter enormously and yet be within the bounds of normality. If those who use these models will bear this in mind and will impress this fact on their students, they can be used with safety for teaching purposes. If, however, they are used as standards for descriptive purposes, perhaps even with measurements and capacities, etc., they will but perpetuate in a new form those cast-iron descriptions which were simple and easy for a student to learn, but which gave a habit of mind in clinical work that was, to me at any rate, a great obstacle to gaining an understanding of the things which one saw in the living anatomy when one came to study it by means of X-rays. The effect of this descriptive teaching of anatomy runs into the clinical medicine books—surely the student who has never seen a stomach filled with opaque food must imagine a *dilated* stomach as something resembling a distended football bladder, whereas, being a potential cavity, the normal stomach is canalised, *i.e.* "dilated" with quite a small quantity of food and gradually distends as more food is taken, the walls being contracted on the contents at all stages. The "dilated" stomach is one found in everyday life after a full meal has gone into a perfectly normal, well-toned stomach. What is always described as a "dilated stomach," is found in the dyspeptic who eats very little, and is simply an atonic stomach, one in which the tone being defective, the food goes to the bottom and hangs at the lowest part of the sac. In the middle portion, the walls are actually in contact—the cavity is certainly not dilated. "Dilatation" can occur in such a stomach, but the quantity of food to produce such a result would make the most experienced gourmond feel very unhappy. This one instance should be sufficient to make the teacher of anatomy hesitate before he imprints on the student's mind a cast-iron picture of living organs—it requires a re-education for the student to grasp the essential motility and adaptability of the living alimentary tract and his powers of observation and deduction will be hopelessly at sea until he appreciates these facts.

The best method of teaching the anatomy of the living stomach is by demonstrations to small numbers in a good X-ray department, but woe betide that demonstrator who thinks that because the laboratory boy is healthy, his stomach is one that is quite normal and will correspond to the models—the demonstrator may be badly "let down" if his laboratory boy is a little nervous, or finds the food distasteful and nauseous. A true idea of the normal stomach can only be obtained by a long experience of a large number of examinations, and it is only in view of my very large experience, that I venture to write this description for a journal of a science in which I make no pretensions to be an expert.

In the foregoing I have endeavoured to indicate the fact that the stomach is a "fluid" organ, if one may use the term in this sense. It may be displaced across the abdomen by a collection of gas in the colon; it is easily pushed upwards by pelvic tumours, pressure on the abdomen, etc., and in spite of

quite gross displacements it may give not the slightest sign that the distortion is causing any embarrassment of its functions. How some of the ladies existed who "tight-laced," and thus nipped atonic stomachs in the middle, is a problem which, when this fashion recurs, will be worth studying. The fact that this did happen, and that there are survivors to tell the tale, is sufficient to show how wonderful is the adaptability of that organ which, in my student days, I regarded as a retort in which various test-tube experiments were always in progress.

The nearest approach to a fixed point is the cardiac orifice, and since this is incorporated with the diaphragm, and as the fundus of the stomach extends into the left dome, perhaps one should begin with this structure.

The levels given as the results of X-ray findings are from observations in the upright position. So far as my records go they are not materially altered (½ to ¾ inch) by the change to the recumbent position.

I give below a table of levels gathered for me by Dr J. B. Higgins from various works on Anatomy.

	Right	Left	Cardiac orifice	Pylorus
Quain	8th D. V	9th D. V	10th D. V	12th D. V
Text-Book of Anatomy, Gray ...	8th D. V	8–9th D. V	10th D. V	1st L. V
Text-Book of Anatomy, Cunningham	8th D. V	9th D. V	11th D. V	—
Manual of Anatomy, Buchanan ...	8th D. V	9th D. V	11th D. V	1st L. V
Practical Anatomy, Fagge	—	—	11th D. V	1st L. V
Practical Anatomy, Cunningham ...	7th D. V (on forced respiration)	8th D. V	10th D. V	—
Surface Markings, Rawlings... ...	7–8th D. V	8th D. V	11th D. V	1st L. V
Symington's *Atlas*	10th D. V	10–11th D. V	11th D. V	1st, 2nd L. V
Todd's *Clinical Anatomy*	9–10th D. V	—	11th D. V	2nd, 3rd L. V
X-ray	10–11th D. V	11th D. V	12th D. V	3rd L. V

I wish it to be very clearly understood that I am not quoting these figures in any way in disparagement of the great anatomists whose data I am giving. I am quoting them simply to drive home the lesson that the anatomy of the living and of the dead are two very different things and, to the medical student at any rate, it is the anatomy of the living that is of value.

The disparity in the figures is very striking (except in Todd's *Clinical Anatomy* in which his figures were taken from X-ray findings) and is of course due to post-mortem effects. If the figures had been taken from subjects who had died and been preserved in the upright position, an exactly opposite disparity would have resulted, for, tone having disappeared, the action of gravity would have made the diaphragm and all the viscera sag into the abdomen, the stomach and intestines hanging by their attachments or resting on the pelvic floor, with the lower abdomen comparatively bellied out and the upper abdomen comparatively sucked in.

The ziphi-sternal notch corresponds to the mean level of the diaphragm in a large proportion of normal subjects but is not sufficiently constant for a definite landmark.

The level of the umbilicus is usually given as the 3rd L. V. Radiographically it is almost invariably about the lower level of the 4th L. V.

As to the models themselves. They are not taken from any one subject, but are compiled reconstructions, founded on experience. For the purposes of the work however I made a series of special examinations several years ago, taking plates in five positions, *i.e.* (1) standing postero-anterior, (2) standing sideways, (3) lying on back, (4) lying on right side, (5) lying on left side, with a number of normal subjects, whose good nature and scientific interest I willingly acknowledge. On these plates I outlined those portions of the stomach which contained either bismuth or air and filled in the intervening gaps to the best of my ability. In the normal empty stomach one had to rely on rapid glances as the patient took a watery suspension of barium, watching the way in which the rugae were outlined and various other points, before one ventured on making a model of an organ which had to be reconstructed almost entirely from deduction as to the manner in which it filled.

The outlined plates were then placed on a viewing box and pantograph tracings, reduced to one-fifth, were made on cards so that the whole of the records of each position could be seen at a glance. Small size plasticine models were then constructed and these served my own purpose for demonstration. Professor Stopford suggested that they would be more useful natural size and accordingly this has been done.

I do not know of any other models of the normal stomach based on X-ray findings except Jefferson's, which were made chiefly from the cinematographic diagrams published by Groedel. The only attempts to indicate the shape of the normal stomach in the right and left lateral positions that I have come across are in Forssell's admirable book[1]. I did not see these till after I had made my models and it is interesting to note that our ideas on the subject correspond so closely.

THE MODELS

In this description I am purposely avoiding all reference to other viscera, since the radiologist is unable to see these sufficiently clearly to make accurate observations. Most of the viscera of importance from a diagnostic point of view however are comparatively fixed, and we know their positions.

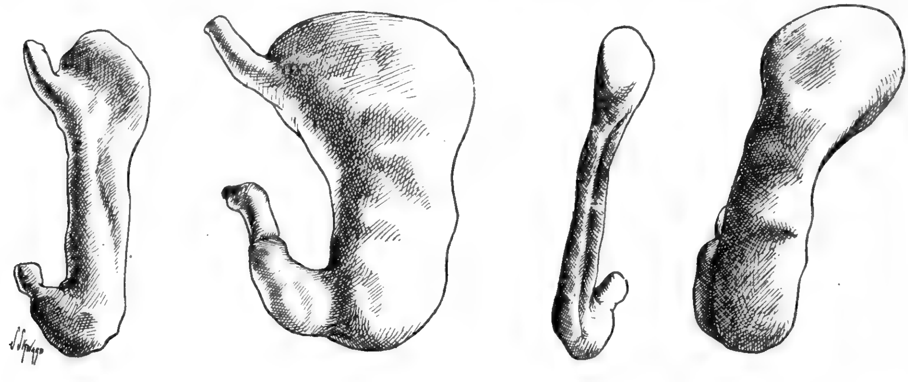
In the series I have included a model of an atonic stomach—one in which the condition is very pronounced. Atony is responsible for such extraordinary changes in the X-ray appearance of the stomach and may be such a transitory condition that it cannot be regarded as a pathological state. Rather it is a physiological relaxation of muscle tone. In order to give the contrast I have also included a model of gastroptosis.

In each case, when speaking of the full stomach, I do not mean a distended organ but one that is comfortably filled by about three-quarters of a pint of food.

[1] *Archiv und Atlas der Normalen und Pathalogischen Anatomie*, 1913.

In order to avoid complicating the models, I have left out all suggestion of peristaltic waves.

In the upright position the *angle of inclination* of the stomach from the fundus downwards is approximately 30 degrees. This was the figure arrived at after 100 consecutive observations. In some subjects however there is practically no angle at all, the organ simply hangs straight down. These are, for the most part, the atonic stomachs found in tall thin women with flat abdomen and poor lumbar curvature. In others there is as great an angle as 60 degrees. These rarer cases are the very hypertonic stomachs met with in short stout men, with rather marked lumbar curvatures, and in whom the



1. 2. 1A. 2A.

Fig. 1. Model of normal empty stomach in upright posture, as seen on its anterior or ventral surface.

Fig. 2. Model of normal stomach moderately filled in upright posture, as seen on its anterior or ventral surface.

Fig. 1 A. Model of normal empty stomach in upright posture, as seen on its left or convex border.

Fig. 2 A. Model of normal stomach moderately filled in upright posture, as seen on its left border or greater curvature.

The drawings are designed merely to show the form of the stomach under the various conditions mentioned in the text; no attempt has been made to represent their relationship to the sagittal median plane of the body.

abdominal fat is well developed. These are the extremes, but a very large proportion of patients, especially with so-called "normal" stomachs, exhibit an angle of about 30 degrees.

There is usually a slight angle in the stomach itself as it comes forward over the kidney. In some subjects, nearly always men, this angle is quite sharp, the upper portion being at an angle of perhaps 70 degrees while the lower two-thirds of the organ drop practically straight down. In these cases the manner in which the stomach fills is peculiar: the upper cup fills first and appears to spill over into the lower part, the "cup and spill type" I always call it. It is a curious angle and is often associated with duodenal lesions. It is certainly due to a spasmodic contraction, but the mechanism

that produces the deformity is not at all easy to understand. Sometimes this angulation is so pronounced that a definite hour-glass contraction is produced.

In children, the stomach is relatively shorter and wider in proportion to the length of the body. Whereas in the adult the stomach reaches the umbilicus, in children up to about four years of age it only comes half way and does not reach the umbilical level till near puberty.

The hypertonic stomach does not differ essentially from the normal—it is proportionally shorter and wider and the pylorus and first part of the duodenum pass more or less transversely, or even downwards, into the second part of the duodenum.

(1) *The normal empty stomach.* (*Standing position.*)

The cardiac end of the stomach naturally varies in size according to the quantity of air contained in it. When there is no fluid at all the air gives a round clear area, but if there is, as is usual, just a little secretion present, the air space will be the arc of a circle with the lower margin a straight fluid line.

The construction of this model is almost entirely from deductions, since the empty stomach cannot be seen. Jefferson[1] studied the canalisation of the empty stomach and found that the liquid food passed down the lesser curvature. He attributed this to the very marked band of oblique fibres that, curving over the cardiac orifice, runs down on either side of the lesser curvature, forming more or less the "canalis gastricus" described by Lewis. These observations I have confirmed, but whether Jefferson's explanation is correct or not I cannot say. My own impressions are rather in the direction that it is simply the fact that the lesser curvature route is the straightest in the line of the action of gravity that causes fluid to take this route. It is quite certain however that there is no *definite* channel down the lesser curvature in the empty stomach, as can readily be shown by giving a spoonful of solid food, as solid as the patient can swallow, and following this up by a watery suspension of barium, when the watery fluid will most likely take an outer course down between the rugae, which can usually be seen as separate shadowy lines, some seven or eight in number, running straight down to the lowest part of the stomach.

The pyloric end cannot be studied until sufficient food has been given to fill it. Therefore this is constructed entirely from deductions from the way in which it fills.

(2) *The normal full stomach.* (*Standing position.*)

As filling takes place, the increased capacity is obtained almost entirely by a widening of the tube. In the model the cardiac end is rather wider than normal, suggesting that the patient has swallowed a fair quantity of air with the food—a perfectly normal act up to a point.

[1] *Archives of the Roentgen Ray*, May 1915.

It will be noted that with moderate quantities of food the capacity is obtained not by increase in the length but almost exclusively by lateral expansion. The organ maintains its contents in tubular form and this tube widens out as more food is taken. This maintenance of the tubular form is the function of the tonic action of the walls and is automatic. It is compensatory to the action of gravity on the contents. In the recumbent position this action is not called into play to counteract gravity and to a large extent disappears. It is a very sensitive action and is evidently controlled centrally. Mental disturbances such as fear and other emotions are at once shown by a relaxation of the tone of the muscle and a consequent drop in the level of the lowest part of the outline. Most of us know the sinking sensation in the abdomen of the waiting period before an examination or a race. This is nothing more than loss of tonic action from emotional causes and is seen very frequently in an X-ray department at the first examination but often disappears at subsequent examinations when the patient is no longer nervous about the procedure.

Naturally the upper portion of the stomach moves with respiration but the lower part does not move appreciably unless with very forced respiration. In an athlete in good condition even forced respiration will hardly move the lower border. Movement of the lower border of the stomach with respiration is one of the early signs of atony. In short, the tonic action is automatic and not only counteracts gravity but also compensates for diaphragmatic movement, maintaining a concertina type of construction in response to the diaphragmatic movement in order to keep the lower part of the stomach in a definite and more or less fixed position.

The normal stomach depends for its shape very largely on the tonic action, and a healthy well-toned stomach shows far less alteration in shape from changes in posture than one in which tone is defective. In the models of the stomach in the Right and Left recumbent postures I have represented the changes one finds in an average healthy stomach—it is probable that in a healthy athletic youth the changes would not be quite so marked, but in a slightly atonic stomach they are far more pronounced than in the models.

(3) *The normal full stomach.* (*Patient lying on the back.*)

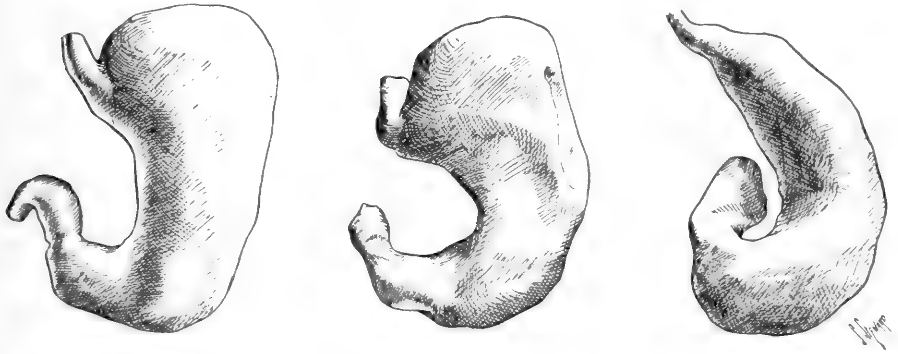
The cardiac end of the stomach, being the lowest part, contains the greater part of the food. Usually there is none remaining in the pyloric half, which is collapsed and lies across the vertebral column. The air in the stomach lies below the abdominal wall and does not necessarily indicate more than a small extent of the stomach—it is only when there is a considerable quantity present that it fills the portion that crosses the middle line, chiefly because of the weight of the abdominal wall, etc. which presses it out of this portion into the part where there is more room and less resistance from behind.

The pyloric end however is easily filled by making the patient lie on the

right side, applying slight pressure over the umbilical region while he turns again on to his back. In this way the pyloric end and the duodenum are very satisfactorily filled and can be studied for diagnostic purposes.

(4) *The full normal stomach.* (*Patient lying on the left side.*)

The whole stomach falls by the action of gravity into the left side of the abdomen, against the abdominal wall. The pylorus is drawn over the vertebral column as far as its attachments will allow and, radiographically, one cannot detect the outline of the pyloric portion of the lesser curvature unless there happens to be a fair quantity of air present. Sometimes one can just detect the pyloric end but, usually, its position can only be located from the shadow remaining in the first part of the duodenum.



3. 4 5.

Fig. 3. Anterior or ventral surface of normal full stomach, patient supine; pyloric end is flattened out and contains no food.

Fig. 4. Anterior or ventral surface of normal full stomach, patient lying on left side.

Fig. 5. Anterior or ventral surface of normal full stomach, patient lying on right side.

(5) *The normal stomach.* (*Patient lying on the right side.*)

In this case the action of gravity draws the stomach right into or even across the middle line. The weight of the food drags on the stomach and pulls on the greater curvature, dragging it out of the dome of the diaphragm. The pyloric end widens to accommodate the food and fully a half of the organ is across the middle line. This results in the pyloric end being to the right of the first part of the duodenum and the pylorus is directed backwards and to the left.

Whether the weight of ordinary food would produce such a marked result as that obtained by examination after the heavy barium meals, is a question which I cannot answer, but my impression is strong that, if the comparison could be made, the difference in resulting shape would be comparatively small.

(6) *Atonic stomach.* ("*Full" of food and patient standing.*)

The condition indicated by the model is one of *marked* atony. The lower border of the stomach would be about 4 inches below the umbilicus and would give a broad crescentic outline.

The middle portion of the stomach is completely collapsed and the food hangs in the lower part as in a toneless bag. There is no effort on the part of the stomach to hold its contents up in tubular form, in fact a part of the weight of the contents may even be taken by the contents of the pelvis. There is generally a considerable quantity of ordinary food, which does not show, lying above the opaque food, but the general outline can be gathered by palpation and splashing of the opaque food up along the walls and by watching

3A. 4A. 5A.

Figs. 3 A, 4 A, 5 A. Profile views of the models shown in full view in Figs. 3, 4 and 5. (Fig. 3 A does not show the flattened and empty condition of the pyloric end as the organ is curved forwards round the vertebrae, etc.)

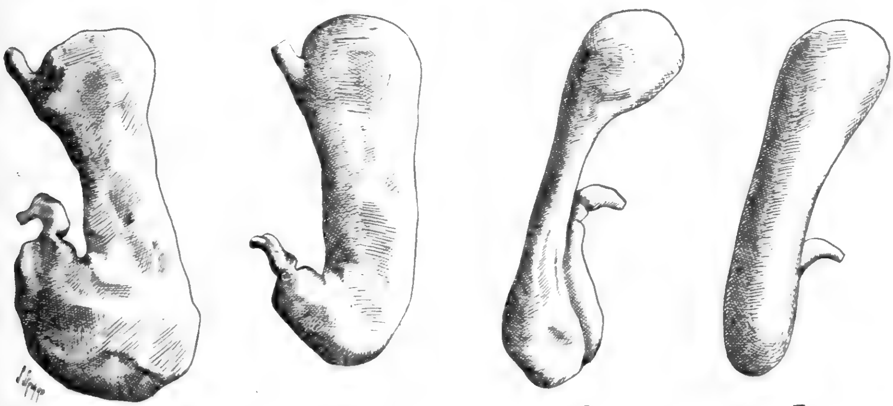
and palpating as new food enters. The pylorus remains in the normal position, high above the lowest part of the stomach. Hence there is mechanical difficulty in emptying.

The weight of the food (and in this case one knows that it is the weight of the ordinary food, since the addition of the opaque meal makes little or no difference) drags on the stomach and stretches the greater curvature. The middle portion of the stomach is collapsed and the anterior and posterior walls, being in contact, offer some slight resistance to the downward passage of opaque food which collects in a funnel shape, and, having canalised the collapsed walls, breaks off in big "blobs" which drop down through the retained food to mix with the heavier opaque food that lies at the bottom of the stomach.

The drag from the weight of the food in the lower part of the stomach makes the shape of the air space characteristic; it is always pyriform, with just a narrow fluid line at the lowest edge.

In many cases one cannot tell whether this type of stomach is a *result* of obstruction or the *cause* of delay in emptying. It may be that at some period

there has been difficulty in emptying, of a transitory nature, perhaps due to defective gastric movements and this has led to retention of food. Tonic action in holding the food up in tabular form is called on too long and the stomach drops, as tone relaxes. This in turn gives rise to difficulty in emptying the stomach, with the result that a temporary loss of tone may give place to a chronic condition, with marked delay in emptying and giving all the X-ray appearances of a typical pyloric obstruction. It is however *atony that is the cause* of the delayed emptying. Exactly the same result and appearance is produced by a pyloric obstruction, giving rise to retention of food and an ultimate defeat of the tonic action of the stomach, *i.e.* in this case the *atony is the effect* of the obstruction.



6. 7 6A 7A

Fig. 6. Full atonic stomach, patient standing.
Fig. 7. Gastroptosis; patient standing, stomach full.
Fig. 6 A. Profile view of Fig. 6.
Fig. 7 A. Profile view of Fig. 7.

(7) *Gastroptosis.* (*Stomach full, patient standing.*)

The essential difference between this condition and the atonic stomach is that tonic action is not lost: it is not a defect in muscular action. Hence the food is held up in tubular form in spite of the fact that the lower border may extend to 5 inches below the umbilicus, *i.e.* almost to the symphysis. It is a long stomach and usually the pylorus is dropped to a considerable extent, together with the kidneys and other organs, *i.e.* it is a part of visceroptosis, Glenard's disease, in which the diaphragm also is below the normal level. But the condition of ptosis may be limited to the stomach, the pylorus retaining its normal position, with the result that there is considerable drag on it and symptoms result. Generally there is no delay in emptying and I have seen a number of patients in whom the condition has given no symptoms. More often however there are symptoms referred to the duodenum. (There is also very frequently some evidence of old appendicular trouble.)

The air space is, as in the normal stomach, the arc of a circle. It must not be overlooked that the two conditions, atony and gastroptosis may, and often do, co-exist, and it is often very difficult to determine how much of the appearances are due to one or other factor.

Note on the alterations in the position of diaphragm and heart from alterations of posture

In making the series of studies necessary for building the models of the stomach in the various bodily positions, I took a large number of radiographs. In each case I had plates of the patient (1) standing straight forward, (2) standing sideways, (3) lying on the back, (4) lying on the left side, (5) lying on the right side.

When engaged in this work I came across the fact, which I had not appreciated myself and which very few of those to whom I spoke seemed to suspect, that the diaphragm and thoracic viscera were capable of considerable movement from alterations of posture. When the patient lay on one side or other, one found that the diaphragm and also the heart and mediastinal contents moved over in accordance with the action of gravity to an extent that was far greater than one would have conceived possible, particularly in patients with relaxed tone.

While publishing an account of the stomach models and while the line of thought is fresh in the reader's mind, I am writing this short note and giving a few of the superimposed diagrams that I obtained during this work. The number of cases examined was not sufficiently large for a detailed study and, when I had done a certain number of cases, I found that there was a fallacy which could not be excluded, *i.e.* that even if a special cage was made in which the patient could lie fixed and in which he could be moved into the various positions, it would be quite impossible to prevent movement of the spine. The slight difference in pose from lying flat on one side or other, on a specially padded board, or the slight rotation of the patient, brought in factors that I could not deal with. Because of the inherent mechanical difficulties the work was abandoned.

The diagrams were produced direct from the X-ray plates taken specially for the purpose. They were outlined with ink on the plates and then pantograph tracings were made, reduced to one in five. These are reproduced without comment as the actual facts recorded, but with the definite statement that although they depict the facts of the movements, there are very considerable faults in technique which render the diagrams of comparatively little value. I do not see how it would be possible to eliminate the skeletal alterations due to pose, even with a cage arrangement. Moreover the yielding of the body within the cage would not only allow alterations of the spine but would also bring in pressure factors that would have an effect that would be far from negligible.

SUMMARY

The stomach has no fixed shape. The normal average approximates to the letter J.

The chief factors that alter the shape are, alterations in tonic action and accumulations of air in intestines, etc.

Alterations of posture, particularly in the recumbent position, bring about very marked alterations in both the shape and position of the organ.

The shapes as made out with opaque meals are the same as those with normal food—the weight of the food makes little or no appreciable difference in the normal stomach. If however there is defective tonic action, the increased weight exaggerates this defect.

The diaphragm does not retain its horizontal position when the patient lies on his side—with the abdominal organs and the thoracic contents it moves considerably with the action of gravity upwards on the side on which the patient lies. The movements of abdominal and thoracic contents are apparently greatest when the general tone of the patient is lowest, while in healthy athletic persons they are comparatively slight.

The Editorial Committee beg to acknowledge the financial aid given by the Medical Research Council in the publication of the following papers which have appeared in this and in the previous numbers of the *Journal*:

"The Maturation of the Human Ovum," by Prof. Arthur Thomson. Vol. LIII, p. 172. 1919.

"The Development of the Uro-genital System in the Marsupialia," by Dr E. Fraser. Vol. LIII, p. 97. 1919.

"The Variations in the Distribution of Cutaneous Nerves," by Dr J. S. B. Stopford. Vol. LIII, p. 14. 1918.

"Studies on the Anatomical Changes which accompany certain Growth-disorders of the Human Body," by Prof. Arthur Keith. Vol. LIV, p. 101. 1920.

"Voluntary Muscular Movements in Cases of Nerve Lesions," by Prof. Wood Jones. Vol. LIV, p. 41. 1919.

The Committee also take this opportunity of acknowledging the aid given by the Finance Committee of the Royal Society in publishing the following papers:

"The Development of the Uro-genital System in the Marsupialia with Special Reference to Trichosurus Vulpecula," by Drs E. Fraser and G. Buchanan. Vol. LIII, p. 35. 1918.

"On the Development of Pericardiaco-Peritoneal Canals in Selachians," by Prof. E. S. Goodrich. Vol. LIII, p. 1. 1918.

"A Preliminary Note on the Morphology of the Corpus Striatum and the Origin of the Neopallium," by Prof. Elliot Smith. Vol. LIII p. 271. 1919.

MOTOR POINTS IN RELATION TO THE SURFACE OF THE BODY

By R. W. REID, M.D., F.R.C.S.

Professor of Anatomy, University of Aberdeen.

Following upon a visit with the late Professor Paterson, University of Liverpool, to the Orthopoedic Hospital at Shepherd's Bush, London, and upon subsequent visits to the Orthopoedic Department of the First Scottish General Hospital in Aberdeen, I was much impressed with the value of electrical methods employed in the diagnosis and treatment of the results of cases of peripheral nerve lesions, and as an anatomist I thought I might do something to help in the matter.

Accordingly I decided to make a special dissection of a subject in order to show the relation of the points of entrance of the nerves into muscles with regard to the surface of the body and then to make the results of this investigation available in a graphic form for those practising these methods.

With this end in view I considered that the best plan was first to make a cast of a subject in its entire state and thereafter to have the subject dissected with the sole purpose of showing the various points where the several nerves entered the muscles and then to relate these points to the surface of the cast. Accordingly a cast was made in the Anatomy Department of this University of one half of a muscular male subject. The body was subsequently dissected in order to expose its muscles with the nerves entering them and then by comparison and measurement the points of entry of nerves into the several muscles were marked on the surface of the cast.

As this cast had unfortunately undergone a certain amount of distortion owing to the flattening of the soft parts by the weight of plaster, I deemed it advisable to make another cast of a living muscular male and to transfer by proportional measurement the marks indicated on the first cast to the surface of the second one. Photographs of the second cast were then made from different points of view as shown in the accompanying Plates XXVI–XXXIV.

Subjoined is a table showing the number of the principal nerve branches entering each muscle together with the approximate places of entry into each muscle. The segments of the spinal cord from which the nerve supplies are derived are also indicated in the table and this information has been obtained from Gray's *Anatomy, Descriptive and Applied,* 19th edition.

It may be mentioned that the markings refer to the special dissection of a single cadaver but by comparison with cadavera which were being dissected in the course of ordinary practical anatomy work, I find that they are not subject to more variation than might be considered normal.

Muscle	Nerve supply	Origin from segments of spinal cord	Number of points of entry into muscle	Place of entry into muscle	Relation to surface of body
Attrahens aurem	Facial	—	1	Superficial surface, middle third	Plates 26, 27
Attollens aurem	Facial	—	1	Superficial surface, middle third	Plates 26, 27
Retrahens aurem	Facial	—	1	Superficial surface, middle third	Plates 26, 29
Orbicularis palpebrarum	Facial	—	4	Deep surface, middle third	Plates 26, 27
Zygomaticus major	Facial	—	1	Deep surface, upper third	Plates 26, 27
Buccinator	Facial	—	3	Superficial surface, middle third	Plates 26, 27
Orbicularis oris	Facial	—	3	Superficial surface, near corner of mouth	Plates 26, 27
Masseter	Inferior maxillary	—	1	Deep surface, just below zygoma	Plates 26, 27
Temporal	Inferior maxillary	—	3	Deep surface, just above zygoma	Plates 26, 27
Platysma myoides	Facial	—	5	Deep surface, upper third	Plates 26, 27
Sterno-mastoid	Spinal accessory; Cervical	1, 2, 3, 4, 5, C.; 2, 3, C.	4	Superficial surface, lower third; Deep surface, middle third	Plates 26, 27
Digastric	Inferior maxillary; Facial	—; —	1; 1	Deep surface, middle third; Superficial surface, upper fifth	Plates 26, 27
Stylo-hyoid	Facial	—	1	Superficial surface, middle third	Plates 26, 27
Sterno-hyoid	Cervical	1, 2, 3, C.	2	Superficial surface, middle third	Plates 26, 27
Sterno-thyroid	Cervical	1, 2, 3, C.	1	Deep surface, lower third	Plates 26, 27
Thyro-hyoid	Cervical	1, 2, C.	1	Superficial surface, upper third	Plates 26, 27
Omohyoid	Cervical	1, 2, 3, C.	2	Deep surface, anterior belly, middle third; Deep surface, posterior belly, upper third	Plates 26, 27
Trapezius	Spinal accessory; Cervical	1, 2, 3, 4, 5, C.; 3, 4, C.	8	Deep surface, middle third	Plate 29
Latissimus dorsi	Long subscapular	5, 6, 7, C.	7	Deep surface, upper third	Plates 27, 29
Rhomboideus major	Cervical	5, C.	2	Deep surface, middle third	Plate 29
Rhomboideus minor	Cervical	5, C.	1	Deep surface, middle third	Plate 29
Pectoralis major	External and internal anterior thoracics	5, 6, 7, 8, C. 1, T.	9	Deep surface, middle third	Plates 26, 27
Pectoralis minor	Internal anterior thoracic	8, C. 1, T.	2	Deep surface, middle third	Plates 26, 27
Subclavius	Cervical	5, 6, C.	1	Deep surface, middle third	Plates 26, 27
Serratus magnus	Long thoracic	5, 6, 7, C.	5	Superficial surface, anterior third	Plates 26, 27
Deltoid	Circumflex	5, 6, C.	8	Deep surface, middle third	Plates 26, 27
Supraspinatus	Suprascapular	5, 6, C.	2	Deep surface, middle third	Plate 29
Infraspinatus	Suprascapular	5, 6, C.	3	Deep surface, middle third	Plate 29
Teres minor	Circumflex	5, C.	3	Deep surface, outer third	Plate 29
Teres major	Lower subscapular	5, 6, C.	3	Deep surface, middle third	Plates 26, 29
Coraco-brachialis	Musculocutaneous	7, C.	2	Deep surface, upper third	Plates 26, 27
Biceps flexor cubiti	Musculocutaneous	5, 6, C.	5	Deep surface, middle third	Plate 27
Brachialis anticus	Musculocutaneous	5, 6, C.	4	Superficial surface, middle third	Plate 27
Triceps extensor	Musculospiral	7, 8, C.	9	Deep surface, upper third	Plate 29
Pronator radii teres	Median	6, C.	2	Deep surface, upper third	Plate 27
Flexor carpi radialis	Median	6, C.	1	Deep surface, upper third	Plates 27, 28

Palmaris longus	Median	6, C.	1	Deep surface, upper third	Plate 27
Flexor carpi ulnaris	Ulnar	8, C. 1, T.	2	Deep surface, upper third	Plates 27, 28
Flexor sublimis digitorum	Median	7, 8, C. 1, T.	5	Deep surface, middle two fourths	Plates 27, 28
Flexor profundus digitorum	Median and ulnar	8, C. 1, T.	6	Superficial surface, upper third	Plates 27, 28
Flexor longus pollicis	Median	8, C. 1, T.	2	Superficial surface, upper third	Plates 27, 28
Pronator quadratus	Median	8, C. 1, T.	1	Deep surface, middle third	Plates 27, 28
Supinator longus	Musculospiral	5, 6, C.	2	Deep surface, upper third	Plate 27
Extensor carpi radialis longior	Musculospiral	6, 7, C.	2	Deep surface, upper third	Plate 27
Extensor carpi radialis brevior	Posterior interosseous	6, 7, C.	2	Deep surface, upper third	Plates 27, 28
Extensor communis digitorum	Posterior interosseous	7, C.	3	Deep surface, upper third	Plate 29
Extensor minimi digiti	Posterior interosseous	7, C.	1	Deep surface, upper third	Plate 29
Extensor carpi ulnaris	Posterior interosseous	7, C.	2	Deep surface, upper third	Plate 29
Anconeus	Musculospiral	7, 8, C.	1	Deep surface, middle third	Plate 29
Supinator brevis	Posterior interosseous	6, C.	1	Superficial surface, upper third	Plates 27, 28
Extensor ossis metacarpi pollicis	Posterior interosseous	7, C.	2	Superficial surface, upper fifth	Plate 29
Extensor primi internodii pollicis	Posterior interosseous	7, C.	1	Deep surface, upper third	Plate 29
Extensor secundi internodii pollicis	Posterior interosseous	7, C.	1	Superficial surface, upper fifth	Plate 29
Extensor indicis	Posterior interosseous	7, C.	1	Deep surface, upper fifth	Plate 29
Abductor pollicis	Median	6, 7, C.	1	Deep surface, upper third	Plates 27, 28
Opponens pollicis	Median	6, 7, C.	1	Deep surface, upper third	Plates 27, 28
Flexor brevis pollicis	Median and ulnar	6, 7, 8, C.	2	Superficial surface, upper third	Plates 27, 28
Adductor obliquus pollicis	Ulnar	8, C.	2	Deep surface, inner fifth	Plates 27, 28
Adductor transversus pollicis	Ulnar	8, C.	1	Deep surface, inner fifth	Plates 27, 28
Abductor minimi digiti	Ulnar	8, C.	2	Deep surface, upper third	Plates 27, 28
Flexor brevis minimi digiti	Ulnar	8, C.	1	Superficial surface, upper third	Plates 27, 28
Opponens minimi digiti	Ulnar	8, C.	1	Deep surface, upper third	Plates 27, 28
Lumbricales	Ulnar	8, C.	2	Deep surface, upper third	Plates 27, 28
	Median	6, 7, C.	3	Superficial surface, upper third	
Interossei	Ulnar	8, C.	7	Palmar surface, upper fifth	Plates 27, 28
Tensor fasciae femoris	Superior gluteal	4, 5, L. 1, S.	1	Deep surface, middle third	Plates 30, 32
Sartorius	Anterior crural	2, 3, 4, L.	7	Deep surface, upper half	Plates 30, 33
Rectus femoris	Anterior crural	2, 3, 4, L.	4	Deep surface, upper half	Plate 30
Vastus externus	Anterior crural	2, 3, 4, L.	5	Superficial surface, upper third	Plates 30, 32
Vastus internus	Anterior crural	2, 3, 4, L.	6	Superficial surface, middle third	Plates 30, 33
Crureus	Anterior crural	2, 3, 4, L.	4	Superficial surface, upper third	Plates 30, 32
Gracilis	Obturator	3, 4, L.	2	Deep surface, upper third	Plates 30, 33
Pectineus	Anterior crural	2, 3, 4, L.	1	Superficial surface, upper third	Plates 30, 33
Adductor longus	Obturator	3, 4, L.	4	Deep surface, middle third	Plates 30, 33
Adductor brevis	Obturator	3, 4, L.	2	Superficial surface, upper third	Plates 30, 33
Adductor magnus	Obturator	3, 4, L.	4	Anterior surface, upper fourth	Plates, 31 33
	Great sciatic	4, 5, L.	3	Posterior surface, middle third	
Gluteus maximus	Inferior gluteal	5, L. 1, 2, S.	5	Deep surface, middle third	Plates 31, 32
Gluteus medius	Superior gluteal	4, 5, L. 1, S.	5	Deep surface, middle third	Plates 31, 32
Gluteus minimus	Superior gluteal	4, 5, L. 1, S.	3	Superficial surface, junction of upper and middle thirds	Plates 31, 32

Muscle	Nerve supply	Origin from segments of spinal cord	Number of points of entry into muscle	Place of entry into muscle	Relation to surface of body
Pyriformis	Sacral plexus	1, 2, S.	1	Anterior surface, inner third	Plates 31, 32
Obturator internus	Sacral plexus	1, 2, 3, S.	1	Superficial intra pelvic surface, near small sciatic notch	Plates 31, 32
Gemellus superior	Sacral plexus	1, 2, 3, S.	1	Superficial surface, junction of inner and middle thirds	Plates 31, 32
Gemellus inferior	Sacral plexus	5, L. 1, S.	1	Deep surface, middle third	Plates 31, 32
Quadratus femoris	Sacral plexus	5, L. 1, S.	1	Deep surface, junction of inner and outer two thirds	Plates 31, 32
Obturator externus	Obturator	3, 4, L.	1	Deep surface, near anterior edge of obturator foramen	Plates 31, 32
Biceps flexor cruris	Great sciatic	4, 5, L. 1, 2, 3, S.	3 3	Deep surface, middle third Superficial surface, upper third	Plates 31, 32
Semitendinosus	Great sciatic	4. 5, L. 1, 2, 3, S.	3	Deep surface, middle third	Plates 31, 33
Semimembranosus	Great sciatic	4, 5, L. 1, 2, 3, S.	3	Deep surface, middle third	Plates 31, 33
Tibialis anticus	Anterior tibial	4, 5, L. 1, S.	4	Deep surface, upper half	Plates 30, 32
Extensor proprius hallucis	Anterior tibial	4, 5, L. 1, S.	1	Superficial surface, upper fifth	Plates 30, 32
Extensor longus digitorum	Anterior tibial	4, 5, L. 1, S.	2	Deep surface, upper half	Plates 30, 32
Peroneus tertius	Anterior tibial	4, 5, L. 1, S.	1	Deep surface, upper fourth	Plates 30, 32
Gastrocnemius	Internal popliteal	1, 2, S.	5	Deep surface, upper fifth	Plates 31, 32
Soleus	Internal popliteal Posterior tibial	1, 2, S. 1, 2, S.	2 3	Superficial surface, upper fifth Deep surface, middle third	Plates 31, 32, 33
Plantaris	Internal popliteal	4, 5, L. 1, S.	1	Deep surface, middle of fleshy belly	Plates 31, 32
Popliteus	Internal popliteal	4, 5, L. 1, S.	1	Deep surface, middle third	Plates 31, 32
Flexor longus hallucis	Posterior tibial	5, L. 1, 2, S.	4	Deep surface, middle two fourths	Plates 31, 32, 33
Flexor longus digitorum	Posterior tibial	5, L. 1, S.	3	Superficial surface, upper third	Plates 31, 33
Tibialis posticus	Posterior tibial	5, L. 1, S.	2	Superficial surface, upper third	Plates 31, 32, 33
Peroneus longus	Musculocutaneous	4, 5, L. 1, S.	4	Deep surface, upper half	Plates 30, 32
Peroneus brevis	Musculocutaneous	4, 5, L. 1, S.	3	Superficial surface, upper half	Plates 31, 32
Extensor brevis digitorum	Anterior tibial	4, 5, L. 1, S.	1	Deep surface, upper third	Plates 30, 32
Abductor hallucis	Internal plantar	5, L. 1, S.	1	Deep surface, upper third	Plate 34
Flexor brevis digitorum	Internal plantar	5, L. 1, S.	3	Deep surface, upper third	Plate 34
Abductor minimi digiti	External plantar	1, 2, S.	1	Deep surface, upper fifth	Plate 34
Flexor accessorius	External plantar	1, 2, S.	1	Superficial surface, upper fifth	Plate 34
Lumbricales	Internal plantar External plantar	5, L. 1, S. 1, 2, S.	4	Deep surface, upper fifth	Plate 34
Flexor brevis hallucis	Internal plantar	5, L. 1, S.	2	Superficial surface, middle third	Plate 34
Adductor obliquus hallucis	External plantar	1, 2, S.	1	Deep surface, upper third	Plate 34
Adductor transversus hallucis	External plantar	1, 2, S.	1	Deep surface, middle third	Plate 34
Flexor brevis minimi digiti	External plantar	1, 2, S.	1	Deep surface, middle third	Plate 34
Interossei dorsal and plantar	External plantar	1, 2, S.	7	Plantar surface, upper fifth	Plate 34

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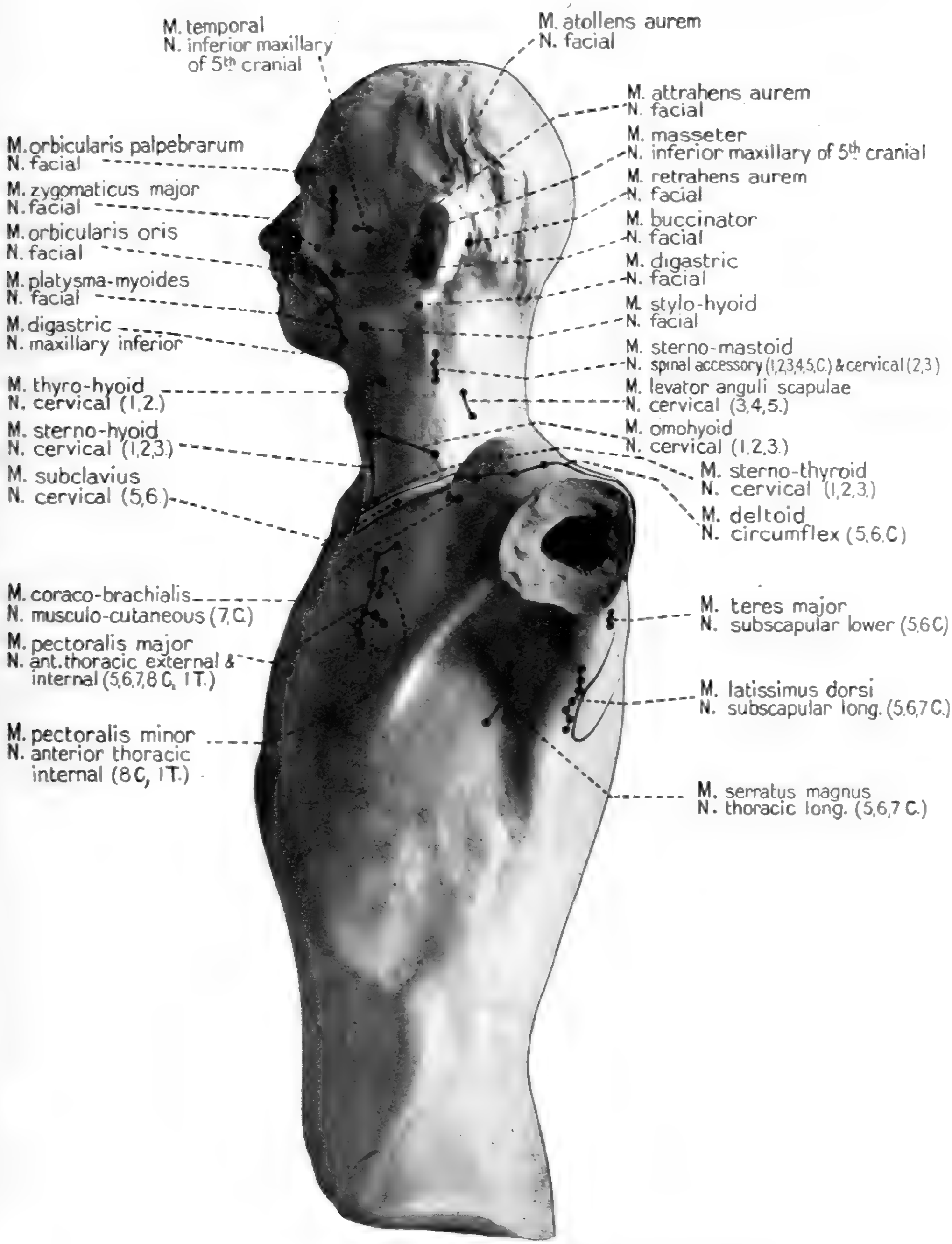

View of cast of trunk of living male from left side showing motor points.

(Prepared in the Anatomy Department of University of Aberdeen.)

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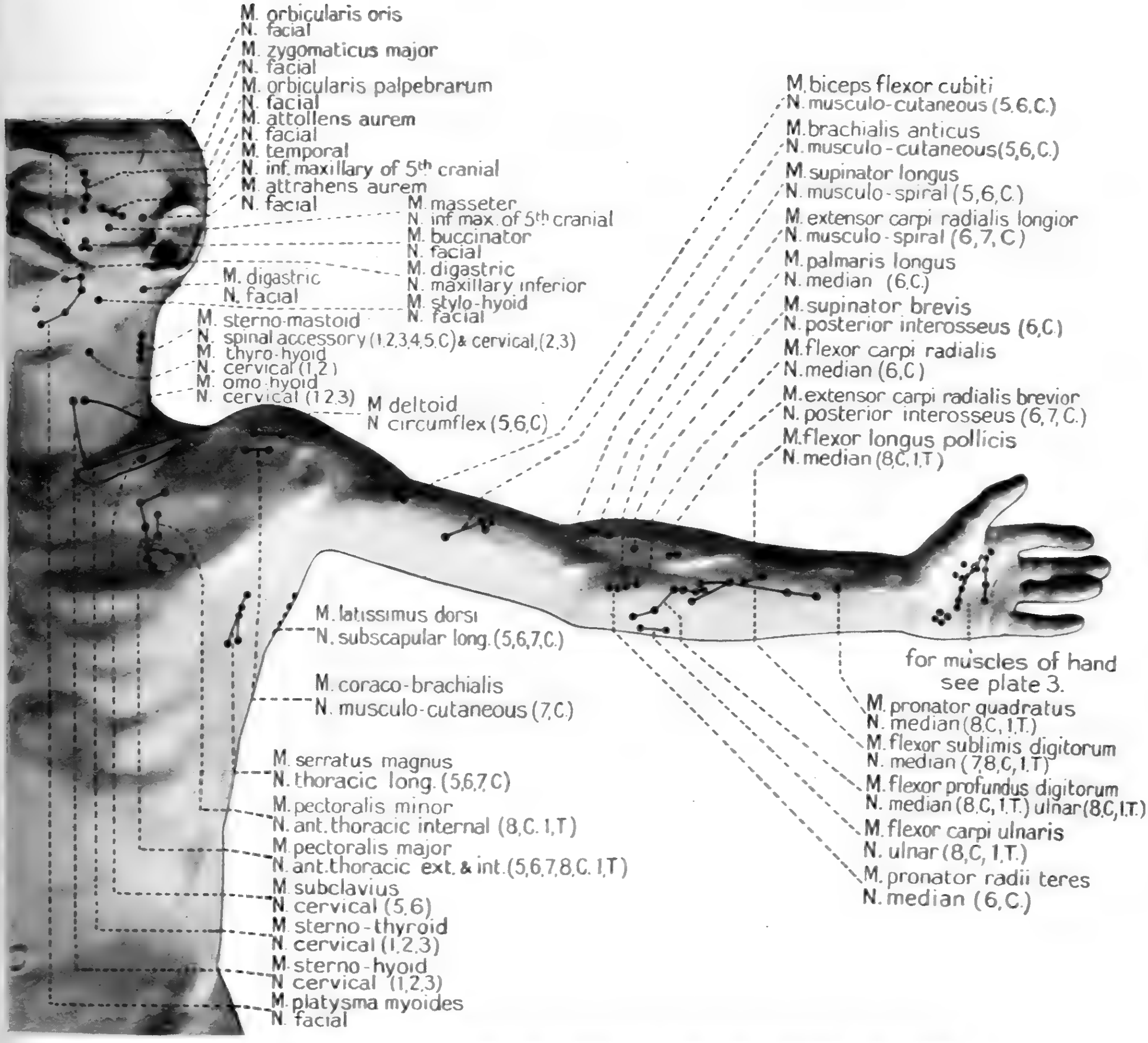
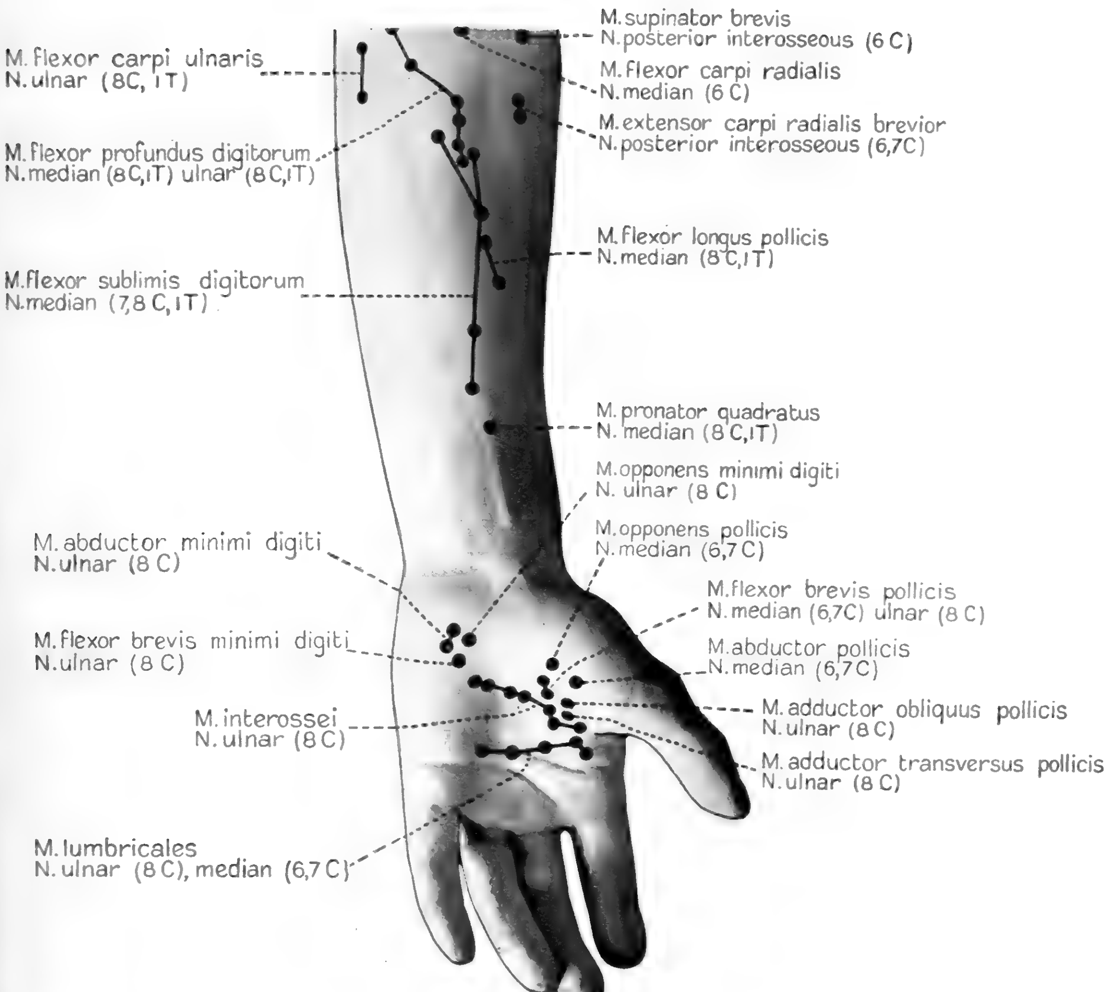


View of cast of left side of trunk and upper extremity from front showing motor points.

(Prepared in the Anatomy Department of University of Aberdeen.)



View of cast of left fore-arm and hand from front showing motor points.
(Prepared in the Anatomy Department of University of Aberdeen.)

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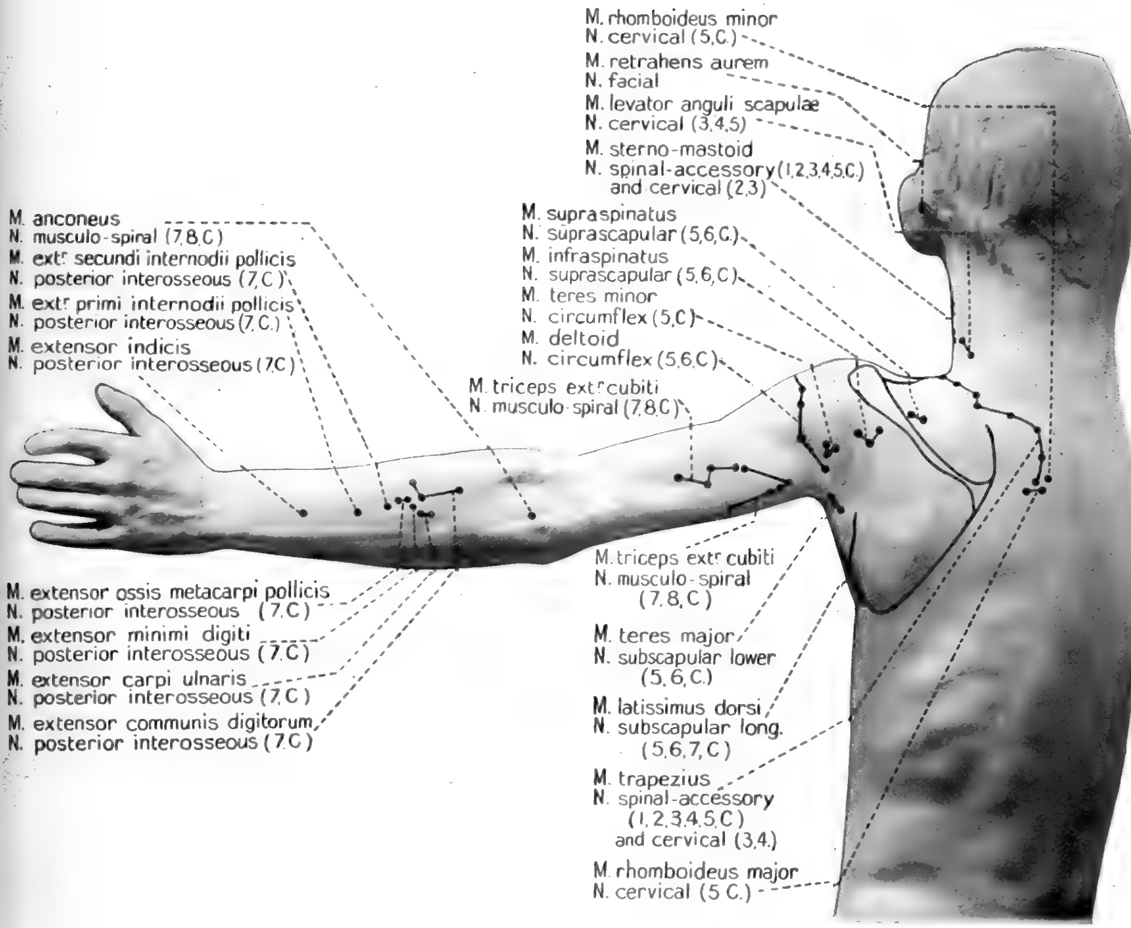

View of cast of left side of trunk and upper extremity from behind showing motor points.

(Prepared in the Anatomy Department of University of Aberdeen.)

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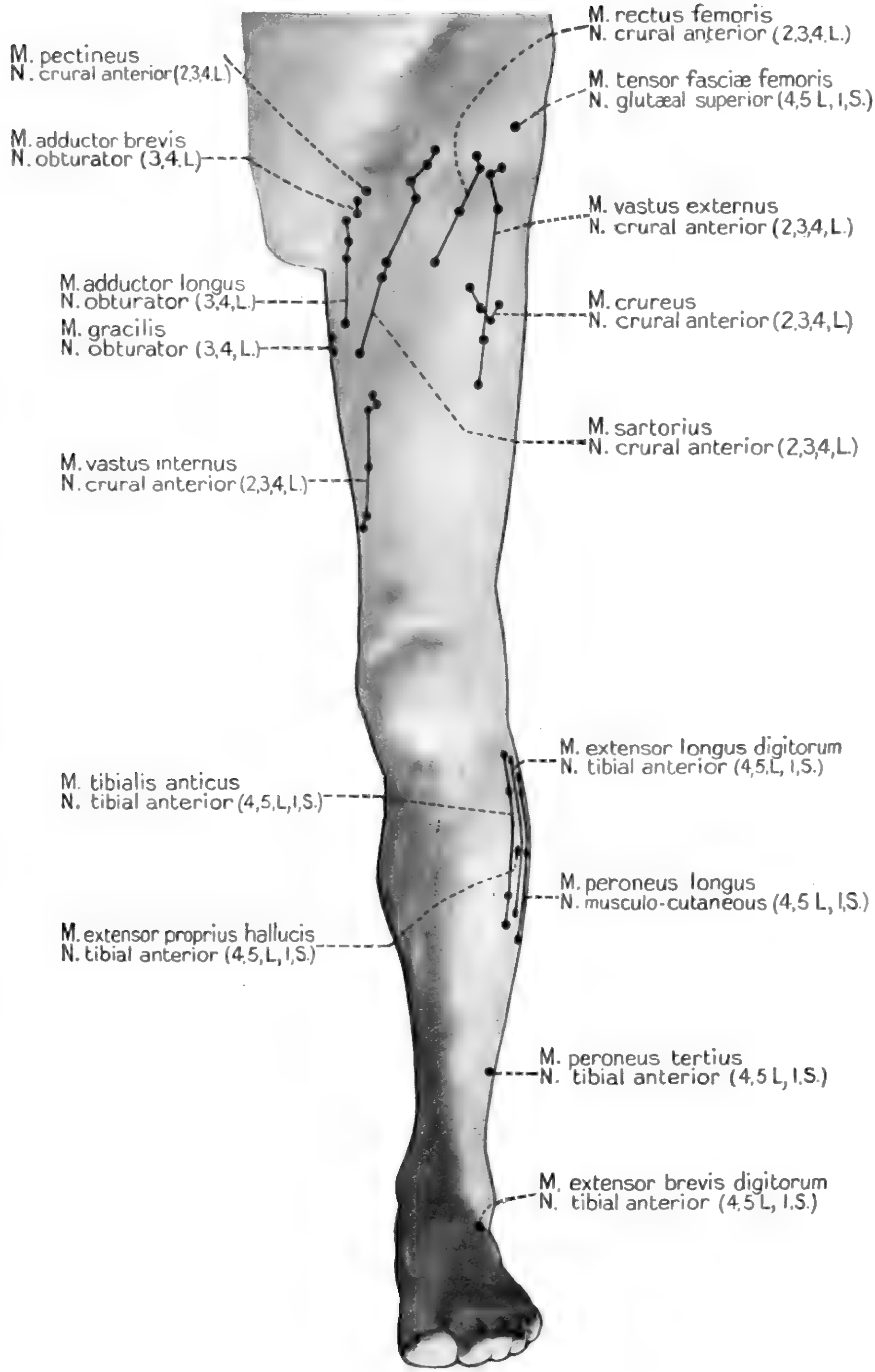

View of cast of left lower extremity from front showing motor points.
(Prepared in the Anatomy Department of the University of Aberdeen.)

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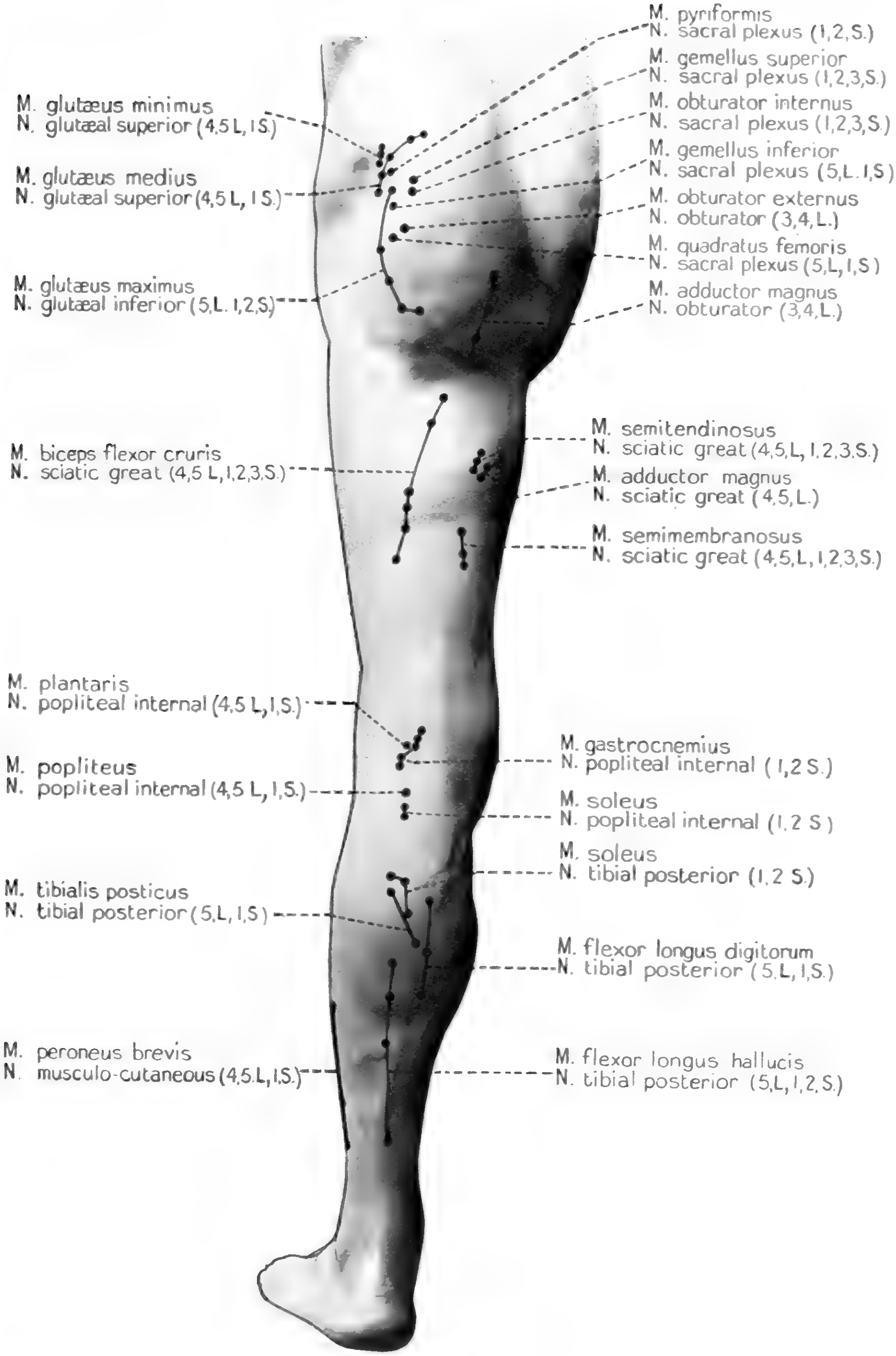
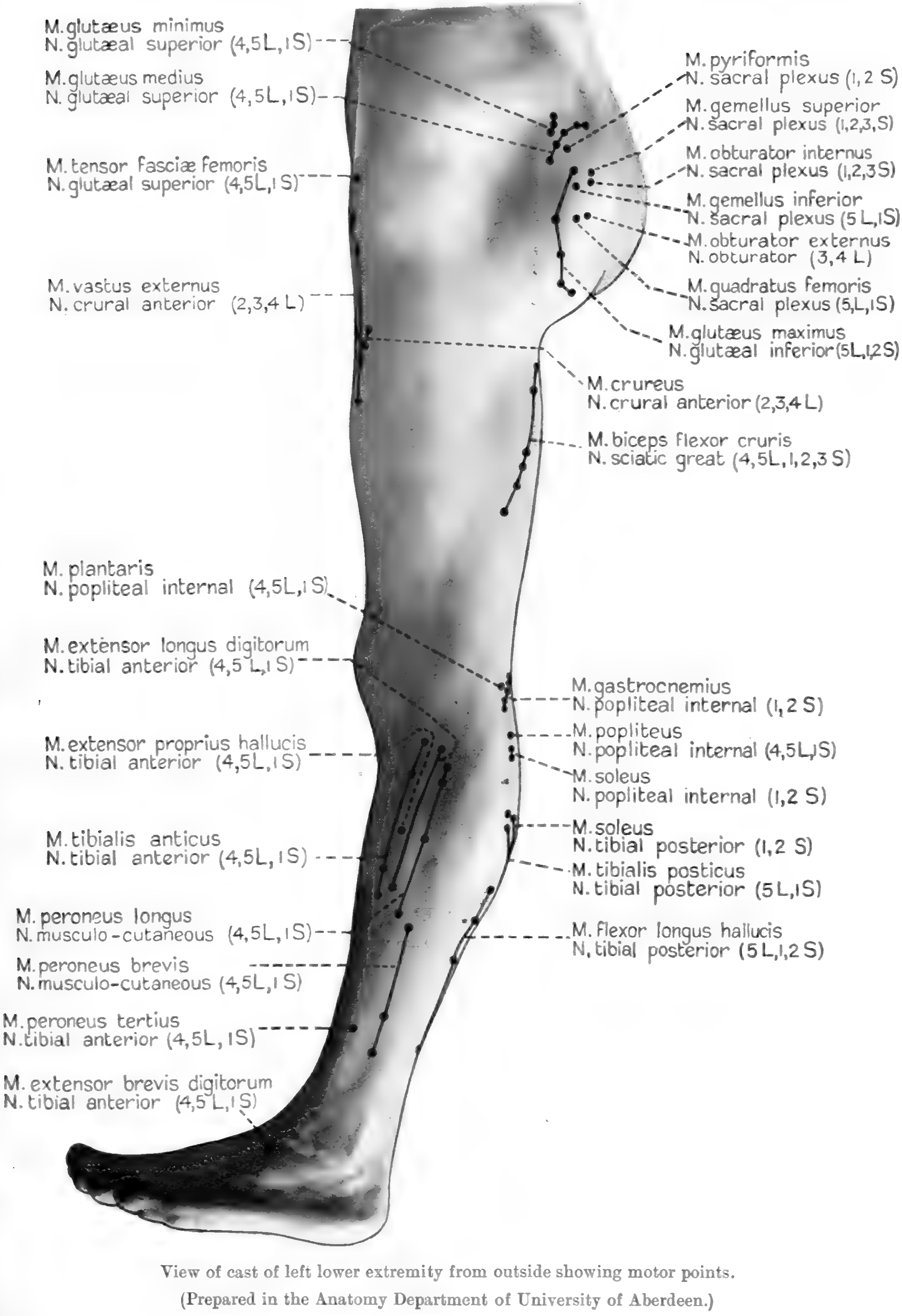


View of cast of left lower extremity from back showing motor points.

(Prepared in the Anatomy Department of University of Aberdeen.)



View of cast of left lower extremity from outside showing motor points.
(Prepared in the Anatomy Department of University of Aberdeen.)

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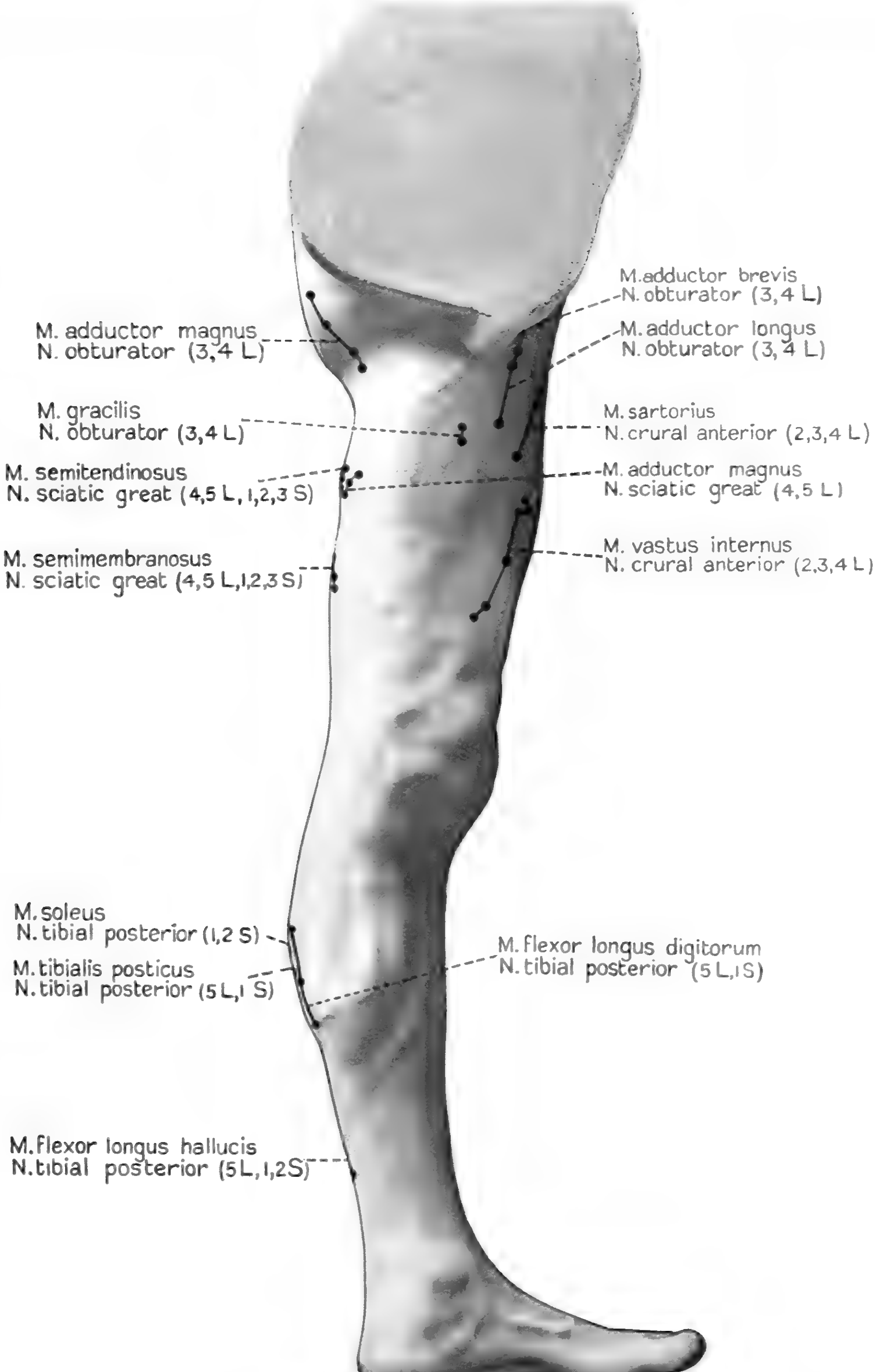
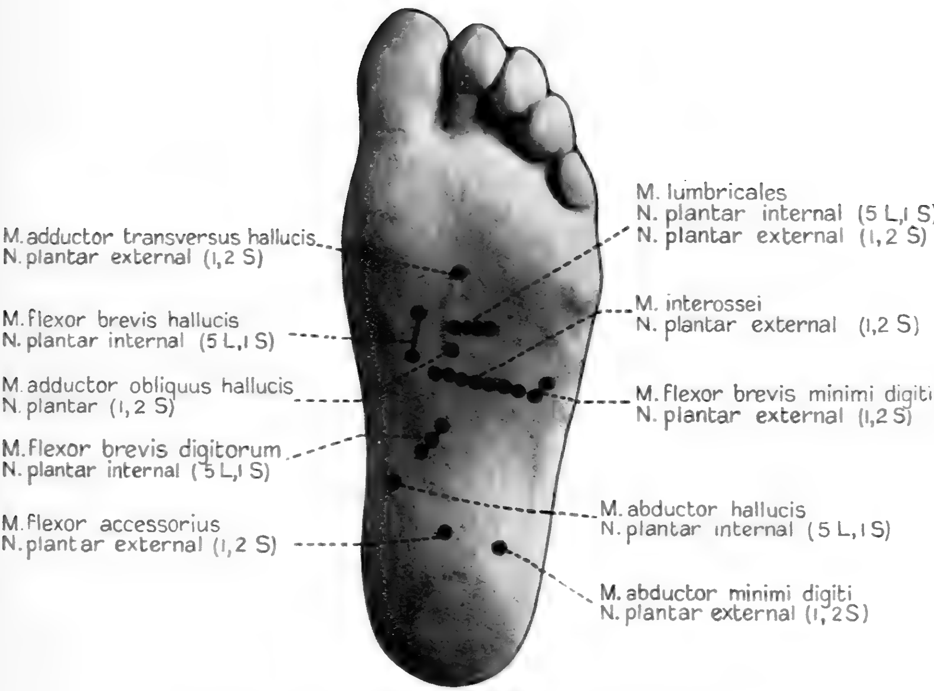


View of cast of left lower extremity from inside showing motor points.
(Prepared in the Anatomy Department of University of Aberdeen.)



View of cast of sole of left foot showing motor points.

(Prepared in the Anatomy Department of University of Aberdeen.)

In making this investigation I wish to acknowledge the assistance given by Mr William Banbury, of the School of Art, Aberdeen, in making the cast which is figured in the Plates and I particularly desire to make mention of the great interest and help rendered by Mr G. O. Thornton, B.A., LL.B., Student of Medicine in this University, especially in the making of the special dissection and in transferring the motor points to the surface of the casts.

I wish, also, to thank Mr George Milne, artist, of the firm of Messrs George Robb, Lithographers, Adelphi, Aberdeen, for the great care he bestowed in connection with the photographing and lettering of the casts.

In the plates the black dots indicate motor points and the black lines indicate groups of motor points.

Copies of the casts marked and lettered in black and red (£13. 13*s*. per set) may be had on application to Messrs Robb, Lithographers, Adelphi, Aberdeen, N.B.

A CASE OF PARTIAL TRANSPOSITION OF THE MESOGASTRIC VISCERA

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INTRODUCTION

The case here recorded is an example of a very rare type of partial heterotaxy, viz., one in which the stomach, duodenum, spleen and pancreas only are involved.

CLINICAL HISTORY

The patient was a boy of 13 who died of acute septico-pyaemia resulting from osteomyelitis of the second left metatarsal bone. Clinically the liver was found to be distinctly enlarged, but the heterotaxy was entirely unsuspected during life.

POST-MORTEM EXAMINATION

The principal lesion present was pyaemic infarction of the lungs. Both organs contained numerous haemorrhagic infarcts of various sizes, the larger especially showing central suppurative softening.

The condition of partial heterotaxy was at once evident on inspection, *in situ*, of the abdominal viscera. The liver was obviously much enlarged, the left lobe being quite as prominent as the right. The stomach was completely transposed, but was otherwise morphologically normal. The fundus lay to the right of the middle line, immediately under the right lobe of the liver, and in relation to it was a bunch of spleens of various sizes. The duodenum passed from the pylorus upwards and to the left, turned acutely downwards, and then to the right. Thereafter it passed upwards, and once more to the left. The pancreas, which appeared greatly shortened, arose from the duodenum at the junction of the first and second parts as above described. It passed almost directly upwards and terminated in the region of the cardiac orifice of the stomach, to which it was firmly adherent. Its total length was slightly under three inches.

None of the other viscera, either thoracic or abdominal, were transposed. The relatively large size of the left lobe of the liver (it was almost as big as the

right) was not found to be associated with any evidence of heterotaxy of that organ.

The stomach, duodenum, spleen and pancreas were removed *en masse* and preserved for subsequent dissection.

DETAILED DESCRIPTION OF THE SPECIMEN

Stomach. The stomach, although lying entirely beneath the liver, exhibits a striking resemblance in shape to the ordinary, moderately contracted, post-mortem stomach, save that it is reversed, the lesser curvature being to the left, the greater curvature to the right. The fundus is well developed. There is a well marked incisura angularis in the lesser curvature rather more than two-thirds of the distance between the cardiac orifice and the pylorus, and there is a more or less definite pyloric antrum on the greater curvature. The pyloric portion exhibits the usual contraction for a distance of 3 cm. from the pylorus.

Duodenum. A statement of the course of the duodenum has been made in the account of the post-mortem examination, and from this it appears that it took the form of a double loop. The concavity of the first loop, very narrow owing to the close apposition of the two limbs in the recent condition, was directed downwards and to the right, and, being in association with the pancreas, represents the ordinary concavity of the first and second portions reversed. The second loop, the concavity of which was directed upwards and to the left, was produced by the third portion of the duodenum passing in more or less normal fashion upwards and to the left to the duodeno-jejunal junction. The first and second portions of the duodenum are in fact reversed, and the transition to the normal arrangement takes place at the junction of the second and third portions. The compressed double loop form of the duodenum is the result.

The body level of the pylorus and the exact position of the duodeno-jejunal junction relative to the posterior abdominal wall were not ascertained.

As a result of this arrangement there is an apparent shortening of the first portion of the duodenum, which extends to the left of the pylorus for about 3 cm. only, just sufficient to allow of the downward bend to the second portion without kinking. The second portion measures about 8 to 9 cm. in length, and the total length of the duodenum is about 24 cm. An examination of the interior of the duodenum lends support to the view that the first portion is shortened. Valvulae conniventes are present to within 1·3 cm. of the pylorus, and the bile papilla (papilla major) is situated at a distance of 5 cm. from the pylorus. The distance of the papilla major from the pylorus varies, according to a number of authors, from 8 to 12 cm. in the adult, and valvulae conniventes do not, as a rule, appear in the normal first portion of the duodenum, i.e., for a distance of about 5 cm. from the pylorus in the adult. The present specimen, however, is from a subject aged 13, and moreover has been preserved by the

Kaiserling process since 1911, so that no doubt some contraction has taken place. On the other hand, as discounting these factors to a considerable extent, the position of the papilla minor relative to the papilla major is of importance. It is situated 2·2 cm. on the pyloric side of the papilla major, the normal variation, according to the same authors, being from 2 to 4 cm. in the adult. Both the papillae are situated on the posterior wall of the second portion o. the duodenum, and their position relative to the circumference of the gut is the reverse of that normally found, the papilla minor being situated 1·2 cm. to the *right* of the papilla major. The papilla major has well marked "hood" and "frenulum" valvulae conniventes; the papilla minor, much less prominent, has a frenulum but no hood.

In two other subjects of the same age (13) the various distances were found to be as follows: pylorus to papilla major, 5·6 cm. and 6·5 cm.; papilla major to papilla minor, 1·5 cm. to 2·5 cm.; pylorus to first vulvula connivens, 2·5 cm. As the duodena from which these measurements were taken had been similarly preserved in formalin, there remains a considerable probability that there is an actual shortening of the first part of the duodenum in the specimen under discussion.

Pancreas. The pancreas is not divisible into head, neck and body, the whole organ being compressed into one mass measuring 7·1 cm. greatest length, by 3·7 cm. greatest breadth. The length of the pancreas is stated in the notes of the post-mortem examination to have been slightly under 3 inches. We have here, therefore, an indication that no serious amount of contraction has since taken place. The long axis lies almost at right angles to the first part of the duodenum, and the blunt extremity is adherent to a number of lymphatic glands matted together on the posterior aspect of the region of the cardiac orifice of the stomach. The lower end of the organ lies behind the first loop formed by the duodenum, and extends more to the right than to the left of its descending portion. It is also closely adherent to the short first portion of the duodenum, and, for a little way, to the lesser curvature of the stomach, coming here into intimate relationship with the bile duct, hepatic artery and portal vein. The pancreas is separated from the nearest spleen by a distance of 2·5 cm.

Ducts of the Pancreas. The main duct (Wirsung), commencing at the upper, blunt extremity, runs downwards nearer to the right than the left border of the organ, bends slightly to the left at the level of the upper border of the first part of the duodenum, and continues downwards in a slightly curved course with the concavity forwards and to the right. Increasing gradually in size it joins the common bile duct as it enters the wall of the duodenum, the junction being effected on the posterior aspect and slightly on the right side of the bile duct. From the point at which the main duct bends to the left the accessory duct (Santorini), continuing the direction of the upper part of the main duct, passes vertically through the right side of the portion of the pancreas adhering to the pyloric region, and opens into the duodenum at the papilla

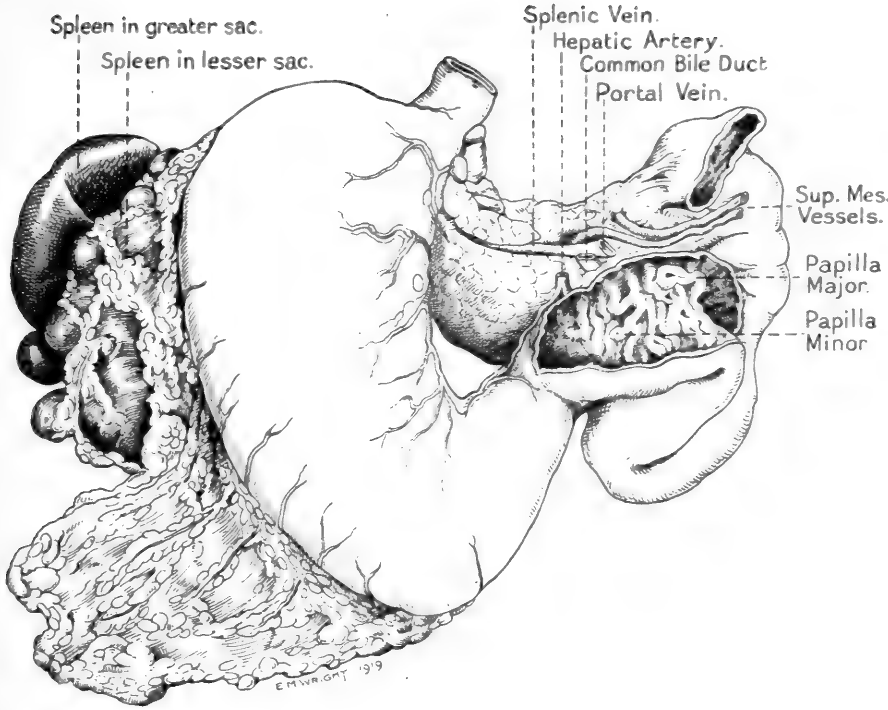

Fig 1. Ventral aspect of specimen.

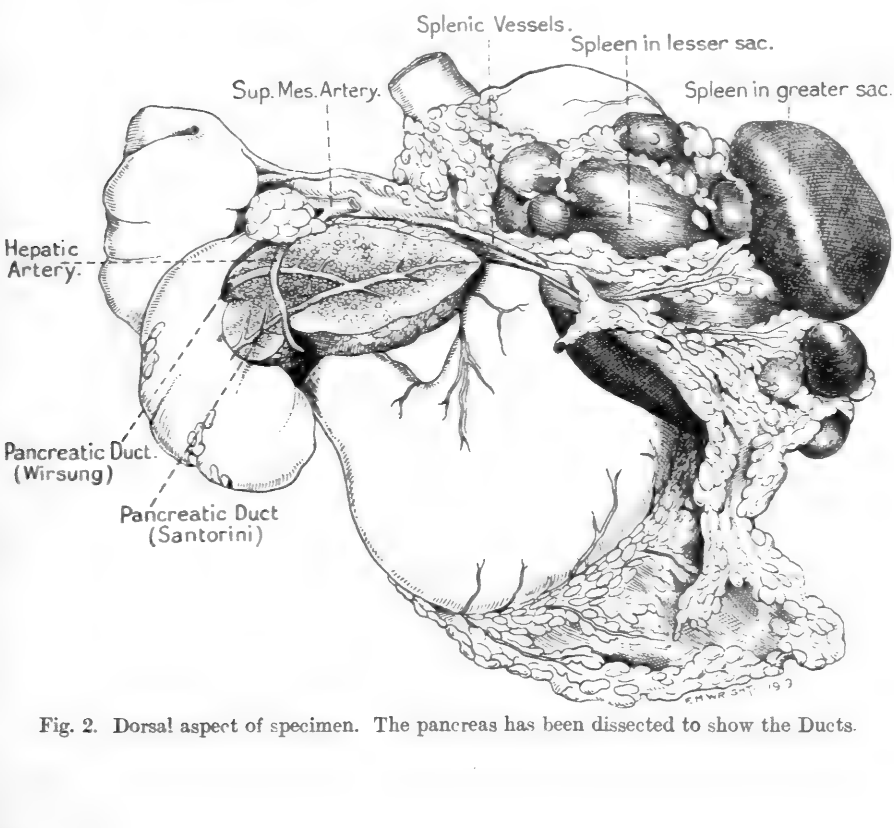

Fig. 2. Dorsal aspect of specimen. The pancreas has been dissected to show the Ducts.

minor. Though varying slightly in size and distinctly narrower as it approaches the gut than at its origin from the main duct, the accessory duct is quite pervious, and readily allows a stylet to be passed through it. Dissected from behind it appears to be the direct continuation of the duct coming from the extremity of the organ, while the actual continuation of the duct of Wirsung apparently springs at an angle from its anterior aspect.

The tributary of the accessory duct, usually described as passing from the lower part of the head of the pancreas upwards in front of the duct of Wirsung, does not appear to be present. Two small tributaries are seen from behind entering the left side of the accessory duct, but neither of these could be traced beyond the line of the main duct.

It would appear therefore that the pancreas shares the incomplete transposition of the duodenum so far as final position is concerned, though developmentally the transposition may be considered to be complete in the sense that the ventral pancreas has rotated with the bile duct to the left instead of to the right. The picture of finally complete transposition could easily be produced in the specimen before us by turning the duodenum more over to the left, and rotating the pancreas to the right behind the body of the stomach. The ducts of the pancreas would then assume their normal positions reversed, and the relative positions of the papillae would similarly become the exact reverse of normal, the minor taking a position ventral to but on the right of the major. It seems probable that this has been prevented by the third portion of the duodenum assuming what is practically its normal position, and so hindering the complete turning over to the left of the second portion.

Spleen. The spleen is divided into thirteen separate portions, two large and eleven small, which lay in the right hypochondrium below the right lobe of the liver. The two larger spleens, measuring respectively 9·2 cm. by 5·6 cm. and 6·1 cm. by 4·1 cm., are closely applied to the greater curvature of the stomach and attached to it by folds of gastro-splenic omentum. The smaller of the two with concave gastric and convex parietal surfaces, lies above and to the right of the larger, and presents the usual relation to the peritoneum, its peritoneal covered surface being visible beyond the greater curvature of the stomach, i.e., in the greater sac. The larger of the two has its peritoneal relations reversed, the peritoneal covered surface being in relation to the posterior surface of the stomach, i.e., in the lesser sac and shut off from the greater sac by the continuation downwards, as the great omentum, of the gastro-splenic omentum attached to the other.

The peritoneal connection of this spleen is more directly with the posterior wall of the lesser sac than with the greater curvature of the stomach, i.e., it is attached to the dorsal mesogastrium dorsal to the smaller spleen, which lay in the greater sac. Its shape is of considerable interest as throwing light upon the factors that probably mould the normally situated organ. The vessels enter the dorsal aspect at a distinct hilum, and the whole dorsal surface, applied to the posterior wall of the lesser sac and in relation, no doubt, to

the right kidney, is markedly concave. The gastric surface on the other hand, though directly applied to the greater curvature and posterior aspect of the stomach, does not appear to be much impressed thereby. It is distinctly convex in all directions, with a slight concavity in the middle. It would appear therefore that the natural growth of the spleen around its entering vessels is to some extent responsible for its final shape. This conclusion is strengthened by an examination of the smaller spleens, which exhibit various stages of the formation of a concave surface on the side of the entering vessels and a convex surface on the other side. This deduction from the appearance of the spleens seems to be justified in spite of the fact that the organs were not hardened *in situ*, and it is reasonable to suppose that the moulding action of the stomach on a normally situated spleen is greatly helped by the natural formation of a concavity on the side of the hilum.

It is further interesting to note that there is a slight notching of the right border of the large spleen in the lesser sac: were the stomach and the dorsal mesogastrium reversed so as to occupy their normal position this border would become the ventral border of a normally situated spleen. None of the other spleens show any sign of notching.

The eleven small spleens, varying in greatest diameter from 4·5 mm. to 19 mm., lie grouped around the larger ones, seven in the greater sac and four in the lesser.

Liver. The general position and appearance of the liver have been described in the account of the post-mortem examination. Its most striking feature is the large size of the left lobe, which apparently extended well into the left hypochondrium, though not so far as to occupy the position of the normally situated spleen. The right lobe, extending into the right hypochondrium, is considerably reduced in vertical depth, being flattened from above downwards by the presence of the subjacent, well developed stomach. The visceral surface presents the usual arrangement of fissures as in a normal right sided organ. The gall bladder lies in a shallow fossa to the right of the umbilical fissure, which is converted by a thick *pons hepatis* into a tunnel giving passage to the ligamentum teres.

The bile passages are normally arranged, and the common bile duct lies in front of and to the right of the hepatic artery in the transverse fissure. As it passes downwards it comes to lie in what has been the free edge of the lesser omentum, and taking up a position to the left of the hepatic artery, it passes behind the short first portion of the duodenum. Thereafter, partially surrounded by processes of the main part of the pancreas, it reaches the posterior wall of the second portion, where it is joined by the main duct of the pancreas before finally piercing the wall of the gut.

Peritoneal Relations. Owing to the presence of adhesions the exact position and relations of the foramen of Winslow were not observed, but there is evidence of a well formed lesser sac, there being only one small adhesion between the posterior surface of the stomach near the cardiac end of the lesser

curvature and the largest of the spleens. The relation of the spleens to the lesser sac has already been described, and the continuity of the gastro-splenic omentum with a well formed great omentum mentioned.

The whole of the duodenum was bound down to the posterior abdominal wall, the first and second portions by their connections with the pancreas, and the third, in the ordinary way, being crossed by the superior mesenteric vessels in their course to the mesentery.

Blood Vessels. The coeliac axis artery divides into the coronary and splenic only. The coronary, running upwards behind the pancreas, supplies a few branches to its upper part. Reaching the lesser curvature at the cardiac orifice, it runs along it in the usual way, dividing into two parallel vessels of which the anterior and larger anastomoses with a pyloric branch of the hepatic artery.

The splenic artery runs to the right behind the pancreas for a short distance, and then behind the peritoneum of the posterior wall of the lesser sac to break up into a number of branches for the various spleens. A few branches reach the greater curvature of the stomach, constituting in the usual way vasa brevia and the gastro-epiploic artery. The main splenic artery is only slightly tortuous as it passes behind the first large spleen, and none of the branches to the individual spleens show any tortuosity at all.

The hepatic artery is derived, not from the coeliac axis, but from the superior mesenteric through an enlarged pancreatico-duodenal arch passing over the back of the lower end of the pancreas. There is no obvious anastomotic branch between the hepatic artery thus formed and the coeliac axis or its branches. As it reaches the first part of the duodenum, where it lies to the right of the common bile duct, the hepatic artery gives off a small pyloric branch, while a branch to the greater curvature of the stomach (to complete the gastro-epiploic anastomosis) springs from the vessel as it lies on the back of the pancreas.

The superior mesenteric artery takes a normal course across the front of the third part of the duodenum, but does not lie behind the pancreas, which is entirely to its right. It gives off the hepatic artery as already described.

The portal vein is formed on the left side of the lower part of the pancreas by the junction of the superior mesenteric vein coming from below and the left, and the splenic vein from above and the right. The termination of the inferior mesenteric vein has not been preserved, but in all probability it joined the superior mesenteric. The splenic vein runs in front of and partly embedded in the pancreas, receiving in its course pancreatic tributaries and the coronary vein. The portal vein so formed turns forward in the left side of the pancreas to reach the back of the first part of the duodenum. Here it lies on the left and partly in front of both the common bile duct and the hepatic artery, but at the portal fissure it is found occupying its usual position behind these structures. In this situation it describes a curve to the right before dividing into its two terminal branches, but otherwise it is quite normal in its distribu-

tion. The right and left portal branches are of nearly equal size, and the ligamentum teres and ligamentum venosum show the usual relation to the left branch.

DISCUSSION

We have before us, therefore, a case of incomplete heterotaxy of the mesogastric organs, and the question of the causation of this rare condition presents itself for discussion(2). It should first be noted that incomplete heterotaxy, apart from abnormalities of the great thoracic vessels only, is much rarer than the complete variety. More than 300 cases of the latter have actually been recorded, and Arneill(1) has demonstrated that many are observed clinically and escape record. He has further shown that the proportion of clinical to post-mortem cases has completely altered. Gruber(5) had collected seventy-nine cases recorded up to 1865, only five or six of which had been observed in life, and Arneill himself, in 1902, had records of forty-four cases, thirty-eight of which were clinical. Of Gruber's seventy-nine cases seventy-one were complete, and the remaining eight were abdominal only and all incomplete. So far as we can ascertain, no case has yet been recorded of transposition of all the abdominal viscera unaccompanied by transposition of the thoracic viscera also. We have been unable to trace all the examples of incomplete abdominal heterotaxy of which mention has been noted during a search through the literature of the subject, but three illustrative cases may be quoted.

In 1894 Launay(7) recorded the discovery in a woman, who died of cancer of the pancreas, of partial transposition very similar to that here described, but with the liver also transposed. He referred to another and similar case recorded by Debouie(4) in 1857, making special note of the fact that in the latter the three parts of the duodenum were found to be "normal." Debouie himself describes the duodenum as having its three portions situated in the exact reverse of the normal position, the concavity of the curve formed by them being directed to the right. As the liver in this case was not transposed, the relative positions of the organs were almost exactly the same as in the present example. The spleen was represented by a reddish spherical tubercle about the size of a cherry stone, and attached to the fundus of the stomach in the right hypochondrium. This case was discovered in a child born a little before term. The spleen in Launay's case consisted of two portions, together about the volume of one normal spleen, situated in the right hypochondrium and attached to the tail of the pancreas and the stomach.

In 1854 Allen Thomson(9) wrote an account of a much more curious and interesting condition where all the organs, thoracic and abdominal, *with the exception of stomach, duodenum, pancreas and spleen* were transposed, the exact opposite of the case here described. The stomach, normally situated, lay beneath the left lobe of the transposed liver, and the duodenum had a doubly looped course almost the reverse of that here described, passing finally to the right to its junction with the transposed jejunum. The pancreas occupied

a position departing only slightly from that of the natural organ in consequence of the deviation of the duodenum, and the spleen, though situated lower than usual, was otherwise normal.

It appears that a definite distinction must be made as regards probable causation between complete and incomplete heterotaxy. The former must be dated back at least to the segmentation of the ovum(3), whereas the latter is more probably conditioned by subsequent anomalies in the development either of a median organ which later becomes asymmetrical, or of originally symmetrical, paired bilateral structures one of which constantly disappears or has a different developmental history from the other. Examples are seen in the cases of partial transposition involving the heart and great vessels. Paired organs which normally have no connection with each other developmentally, e.g. reproductive glands, kidneys, suprarenals, cannot conceivably be transposed except as part of a general transposition of all the organs. In this connection it is interesting to quote the following paragraphs from Allen Thomson:

> It is right to state that in attributing the origin of certain malformations to some original peculiar constitution of the germ, and of others to changes and injuries which are ascertained to occur in the progress of development, to the latter of which divisions the malformation of transposition appears most probably to belong, it is by no means intended to be denied that there may in these cases also be a nisus or predisposition belonging to the germ originally and derived by it possibly like other qualities from hereditary transmission.
>
> In offering such explanation of the origin of malformations I do not profess entirely to discover their cause, but rather attempt to point out that part of the process of development with which they are most intimately and constantly connected.

In each case of partial transposition, therefore, a dynamic is to be sought to account for the more obvious changes, though of necessity the true explanation will only thus be thrown further back.

It is now generally believed that "the individual anlagen of an organism mutually influence one another during development so as to cause the formation of a normal organism" (Keibel(6)), and it seems reasonable to seek the determining condition of partial transposition in the growth of any structure which normally is not associated with the middle line in its development, particularly if there is reason to believe that bilateral rudiments of such a structure exist. The only structure that fulfills these conditions in connection with the mesogastrium is the ventral pancreas: the stomach itself, the duodenum, the liver and the dorsal pancreas are all median structures.

The bilateral origin of the ventral pancreas has been denied, on the ground that in the majority of human embryos studied at the period of its first appearance, an unpaired ventral pancreas is found, situated as a rule in the middle line, in the caudal angle between the hepatic diverticulum and the duodenum. On the other hand there are a number of embryological investigations on record which suggest the occasional presence of bilateral rudiments.

Now in complete heterotaxy the ventral pancreas will be transposed, and if the normally developing ventral pancreas be the right rudiment, then for

the transposed organ the left rudiment will develop, this as a result and as a part of the general mirror-image formation of the body. In a case of partial heterotaxy, on the other hand, involving the pancreas, though the left rudiment of the ventral pancreas will again develop, it will now be part of a local process only. It is suggested that the dynamic of such a partial case as the present, involving the organs of the mesogastrium, may be found in the survival of the left rudiment of the ventral pancreas instead of the right, as is believed usually to be the case.

The observed facts of the relative times at which the developmental happenings concerned occur are, at any rate, not opposed to the possibility which is suggested. The hepatic diverticulum appears in the middle line before the sagittal enlargement of the stomach is indicated, and the rudiment of the ventral pancreas associated with the hepatic diverticulum is already present in the earliest embryo in which the rotation of the stomach has been observed. It is suggested as a possibility that the side of the hepatic diverticulum on which the ventral pancreas develops is the side to which it will move, and that this in turn will affect the twisting of the stomach, and of course the dorsal mesogastrium and subsequently developed spleen. It does not follow that the liver will be affected, since it has already proceeded on its developmental path before the bending over of the bile duct takes place, and similarly the small intestine need not be affected beyond the local displacement due to the transposition of the duodenum. There is no reason why the twisting of the intestinal loop should be affected, as this is a separate phenomenon of later date. If the effect does not extend beyond the duodenum then it is likely that the duodenum itself will be shortened; where it is completely transposed as in Launay's case by doing away with the third portion, where the effect does not extend to the whole duodenum by shortening the first part, as in the present case.

If this hypothesis be correct then the case described by Allen Thomson appears as a remarkable instance of an anomaly within an anomaly. It must be explained as a partial transposition superimposed on a complete transposition, the result being the apparently normal situation of the mesogastric organs.

It should be pointed out that the relative position of the two papillae in the second portion of the duodenum furnishes evidence that the pancreas in the present case is, in fact, transposed; and it is also worth noting that according to Lewis (8) the rotation of the stomach is from the first greater at the pyloric than at the cardiac end.

Multiplicity of spleens has been noted as a common condition in transposition. So far as actual numbers go, the highest number on record (Otto, quoted by Testut) is twenty-three, and the next highest seven (recorded twice by Baillie and Cruveilhier). There were thirteen in the present instance.

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THE PRONEPHROS AND EARLY DEVELOPMENT OF THE MESONEPHROS IN THE CAT

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Comparatively few observations have been made on the early development of the excretory system in the Mammalia. The existence of a pronephros was first recorded in the rabbit and rat by Renson ('83), and later Janosik ('85) described pronephric canals in the rabbit. A more detailed investigation of the anterior end of the excretory organ (called by this author *mesonephros*) in the same animal has been given by Martin ('88), and a few observations were made by Rabl ('96) in 1896. The most complete accounts of the mammalian pronephros are those of Kerens ('07) in both the rabbit and the mole, and of Felix ('12), who has described in some detail both pro- and mesonephros in the human embryo. Embryos of the marmot have been studied by Janosik ('04), and van der Stricht ('13) has recorded the existence of a pronephros in an embryo of the bat, *Rhinolophus hipposideros*.

The anterior end of the organ which gives rise to the Wolffian duct shows varying stages of degeneration in different genera; the course of development is much abbreviated, and events follow each other with great rapidity. The correct interpretation of what takes place is therefore not easy, and whilst more knowledge of the conditions in other mammals is greatly needed, the exact significance of these rudimentary structures can only be appreciated after careful comparison with the corresponding parts of the organ in lower vertebrates.

Owing to the rapidity at which development takes place in early stages, a very complete and well preserved series of embryos is an essential factor for accurate observations. The series of cat embryos in the possession of Professor J. P. Hill, from which my investigations are taken, is an excellent one, and the embryos are mostly in a good state of preservation. I should like to express my gratitude to Professor Hill and to thank him for his kind criticism.

In stages possessing 17 to 35 somites and older, the sequence is a very close one, and moreover consists of many individuals of the same age. It is thus quite adequate for a study of the excretory system during this period. The number of embryos with 9 to 16 somites, during which time the Wolffian duct first makes its appearance, is smaller, and, though fairly complete, does not justify a definite and final conclusion as to the exact mode of origin of the duct at this early stage. The observations of these early stages were made from one

embryo of each of the stages with 8, 9, 10, and 12 somites, two embryos with 14, and two with 16 somites.

These investigations were begun in 1918 during my tenure of a research assistantship under the Department of Scientific and Industrial Research.

I am much indebted to Mr F. Pittock of University College for the beautiful microphotographs on plates XXXVI, XXXVII, and XXXVIII.

DESCRIPTION OF STAGES

8 *to* 10 *somites*. The primordium of the excretory organ in the cat first appears in embryos with 8 to 10 somites. At this stage a central cavity is beginning to appear in the somites, and each one is united with the lateral plate by a narrow somitic stalk or intermediate cell mass. In the more cranial portion, that is opposite the first six somites, the somitic stalk appears to consist of two single layers of cells, separated by a lighter portion extending inwards from the coelom, with indications here and there of a definite lumen. More posteriorly the stalk increases in thickness and more definite cavities can be seen within it, although these never extend into the cavity of the somite itself.

At the anterior end of the 7th somite, almost simultaneously with the formation of the intermediate cell mass, the somatic wall of the latter, about midway between the somite and the lateral plate, becomes slightly thickened, and consists of two or three layers of cells which extend up dorsally towards the ectoderm. The thickening becomes very distinct between the 7th and 8th somites, and forms a marked swelling on the somatic side of the stalk; behind this level it gradually increases in size, becoming more prominent. Plate XXXV, fig. 1, shows the swelling in the region of the 8th somite. Although, perhaps most developed at the cranial end of the 9th somite (plate XXXV, fig. 2), the whole somatic wall of the stalk is much thickened throughout this somite, and at the end of the latter and opposite somite 10 (plate XXXVI, fig. 3) it extends out towards the ectoderm as a definite dorsal outgrowth, which is still well marked posterior to the segmented region of the embryo. Although at the cranial end, opposite somites 7 and 8, the swellings may be slightly more marked at some points than at others, no definite metamerism can be distinguished, the thickenings posteriorly forming a continuous ridge.

At the beginning of the 8th somite for a few sections, and again opposite the 9th, the intermediate cell mass becomes isolated from the somite, and is at the same time marked off from the lateral plate by a constriction; in a cross section through one of these points the mid-region of the stalk appears as a somewhat tubular structure, being composed of cells surrounding a latent lumen (plate XXXV, fig. 1 *a*).

Between the somites and again opposite the middle of each, from the level of the sixth somite backwards, a small portion of the coelom becomes partially cut off from the general body cavity just laterally to the somitic stalk. From

between the 8th and 9th somites backwards to the hinder end of the embryo this portion closes in to form a small vesicular chamber, lying immediately to one side of the thickened region of the intermediate cell mass (plate XXXV, fig. 2, *c.ch.*); in front of the 8th somite cranially this structure is less well developed, and opposite the 6th somite can hardly be distinguished. The cavity of the chamber may occasionally extend inwards into the intermediate cell mass.

12 *somites.* The central cavity of the somite is more distinct, and the hinder end of each is united with the lateral plate by the intermediate cell mass, whilst the mid-region of the somite is again connected with the latter by a few cells. Opposite the 6th somite a few cells extend up dorsally from the somatic layer of the stalk, but these disappear, and no thickening is present in the region of the 7th somite. Opposite the 8th and 9th, the middle portion of the stalk remains attached to the lateral plate in the form of a circular mass as in the last stage, its component cells surrounding a lightly staining area in which a central cavity may be distinctly visible (plate XXXV, fig. 4). From the 8th somite posteriorly, this mass increases in size, its somatic wall thickens and extends out towards the ectoderm. This thickening becomes gradually more conspicuous, continuing throughout somite 10 (plate XXXV, fig. 5), and forming opposite the 11th (plate XXXVI, fig. 6 *a*, 6 *b*) and beginning of the 12th somites a prominent solid outgrowth, which lies closely adjacent to the ectoderm pressing the latter slightly outwards. For some distance behind the segmented region of the embryo, a well marked swelling is to be seen on the somatic side of the intermediate cell mass which is thick in this region. Except opposite the anterior part of the 9th somite, where the swelling appeared to be less marked, no segmentation could be distinguished.

The vesicular chambers, described in the last stage, are now much better developed. They are present opposite somites 10 (plate XXXV, fig. 5), 11 (plate XXXVI, fig. 6 *a*, 6 *b*), and 12, and continue behind the segmented region of the embryo as far back as the shortened primitive streak region or tail bud, forming a series of coelomic chambers, which are becoming separated off from the general body at intervals one behind the other. Some are larger than others, as for example opposite somite 10 (plate XXXV, fig. 5, *c.ch.*) where we find a well marked chamber with a wide central cavity lying ventro-laterally to the thickened portion of the somitic stalk. Fig. 7 *a* and *b* shows the condition near the hinder end of the embryo. I put forward the suggestion, which seems to me a probable one, that these structures represent vestigial pronephric chambers, each one communicating with the general coelom by a peritoneal funnel. In some places, as opposite somite 10, a distinct lumen can be seen passing in from the coelom all along the intermediate cell mass as far as the wall of the somite.

14 *somites.* The sections of this embryo are unfortunately rather oblique, thus making a correct interpretation of the swellings of the intermediate cell mass more difficult in the region of the 8th to the 10th somites on that side.

The pronephric ridge extends from the 8th somite posteriorly. The anterior portion, from the 8th to the mid-region of the 9th somite, is separated from the remainder by a gap of ·04 mm.; behind this gap the ridge extends continuously backwards, gradually increasing in thickness to the end of the 14th somite, marking the limit of the segmented region. Here and there a central cavity may be observed within it. Plate XXXVI, fig. 8, *p.r.* shows the ridge at the level of the 13th somite.

The coelomic chambers, so well developed in the last stage, cannot be recognised anteriorly, but from behind the 10th somite posteriorly there is present what appears as a thickened region of the somitic stalk, somewhat circular in cross section, lying immediately ventro-laterally to the pronephric ridge (plate XXXVI, fig. 8, *th.*). It has a solid connection with the coelomic epithelium, and within it at intervals small central cavities, often very indistinct, may be observed. Opposite this connection a slight groove in the coelomic wall may sometimes be seen. After running for some distance behind the last somite the thickened portion of the stalk disappears, and from this region backwards to near the hinder end of the embryo, we find a series of small coelomic chambers, similar to those of the last stage, in process of separating off from the general body cavity. If we compare fig. 8 with fig. 6 *a* and *b* of the preceding stage, there seems great probability that this thickened region of the stalk represents the united coelomic chambers of the earlier embryo, which have become closed off from the coelom.

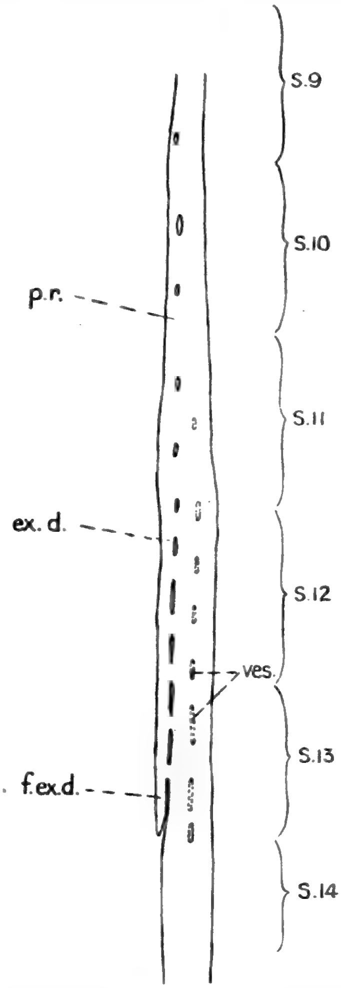
The first indication of the formation of the excretory duct occurs at this stage. On the right side opposite somite 10, the solid dorsal margin of the pronephric ridge is continued backwards for ·03 mm. as a free cellular cord lying close to the ectoderm, the tip of which, only a few cells in thickness, unites once more with the ridge near the end of the somite. Small portions are again separated off from the dorsal margin of the ridge for ·01 or ·02 mm. opposite somites 11 and 12, and at this level they appear to be simply split off at intervals from the ridge, remaining connected with the latter at the intervening points. Whether the condition opposite somite 10, where the distal end of the free portion is distinctly tapering, represents a definite segmental outgrowth, is a question which must be left undetermined until more embryos of exactly this stage are available. In the next stage, an embryo of 16 somites, the dorsal margin of the ridge from near the anterior end of the 13th somite continues posteriorly quite free from the intermediate cell mass as far as the hinder region of the 15th somite. In one embryo of this age, however, its free tip terminates at the level of the anterior end of the 14th somite on the left side. The free portion forms a thin strip of cells, often distinctly tubular, and elongated in a dorso-lateral direction above the somitic stalk.

17 *somites.* The hinder end of each somite is united with the intermediate cell mass, except in the case of the first somite, which is smaller and quite isolated. Opposite the posterior end of the 7th somite there is a slight out-

growth from the dorsal side of the somitic stalk, but this is quite divided off from the ridge behind.

As in the embryo with 14 somites the coelomic chambers have completely disappeared in front of the 11th somite, but from the hinder end of the latter backwards there is present a thickened region of the stalk as described in the last stage. The small central cavities within it have now become more distinct, so that the region from the 11th to the end of the 15th somite takes the form of definite vesicles, attached end to end by solid cellular connections (text-fig. 1, *ves.*). There are two or three vesicles opposite each somite, though they are less developed opposite somite 11; each has a well marked central cavity and is attached to the coelomic epithelium by a solid mass of cells, opposite which a narrow slit-like peritoneal funnel may be present (plate XXXVII, figs. 12 and 13). Behind the level of the 15th somite, the vesicles run back into a solid swollen region of the somitic stalk, and only at about the level at which the 21st somite will later develop do we find small coelomic chambers still being cut off from the general coelom.

The pronephric ridge, from the 8th as far as the anterior portion of the 11th somite, is seen as in preceding stages in the form of a thickening of the intermediate cell mass, but from this level to the end of the 13th somite, where the coelomic chambers have completely closed in, and have become transformed into a longitudinal cord of vesicles, as above described, the ridge passes on to this cord, and appears as a thickening on its dorsal wall, and where vesicles are developed, on the dorsal wall of the latter. This condition is well seen in plate XXXVII, fig. 14, which represents a section through the region of the 12th somite in an older embryo of 19 somites.



TEXT-FIG. 1. Embryo with 17 somites. Diagram of the pronephric ridge (*p.r.*) and primordium of the excretory duct (*ex.d.*), which has split off at intervals from the dorsal side of the ridge. *f.ex.d.* = free distal end of duct. *S* 9, 10, ... = level of somite 9, 10, ... *ves.* = vesicles in the thickened region of the somitic stalk.

The separation of the excretory duct now is more pronounced. At the anterior end of the 8th somite a few cells pass off from the dorsal wall of the thickened side of the stalk and disappear without again uniting with the latter, but posterior to this level

once opposite the end of the 9th somite, twice opposite the 10th (plate XXXVII, fig. 9, *ex.d.*), and three times opposite the 11th and 12th, alternating with the vesicles, the dorsal margin of the ridge becomes split off, anteriorly as a small, posteriorly as a larger mass of cells, elongated in the direction of the long axis of the somitic stalk, and wedged in between the ridge and the ectoderm (text-fig. 1, *ex.d.*). The cells are for the most part radially arranged surrounding either a definite or a latent lumen. Proceeding in the caudal direction, the duct is divided off for longer intervals, so that opposite the 12th somite it is free throughout the greater part of the somite, union only occurring in odd sections. It is, however, very difficult to determine exactly when the duct is completely free, as a dividing line is often not easy to see. The duct is last connected with the ridge at the posterior end of the 13th somite where it terminates on the left, but on the right side it continues back near to the end of the 14th somite as a few cells almost embedded in the ectoderm, the latter at this point being very thin. An excretory tubule later arises opposite each vesicle where the connection with the duct is retained.

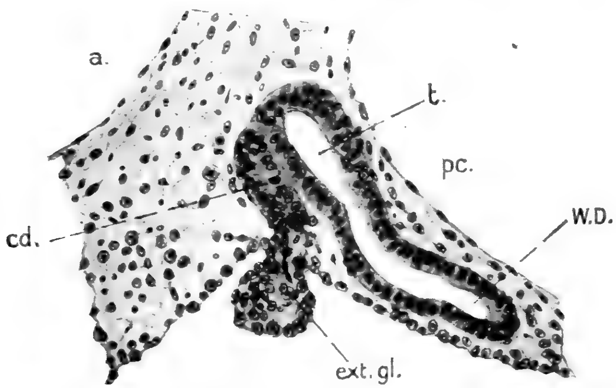
19 *somites*. The cranial end of the excretory primordium is now undergoing degeneration. A small solid outgrowth arises from the intermediate cell mass opposite the anterior portion of the 9th somite, but this is quite disconnected from the rest of the organ, the cranial end of which lies on a level with the hinder end of the 9th somite (plate XXXVIII, fig. 20, *p.r.*). The excretory duct is free behind the end of the 14th somite on the right, and behind the mid-region of this somite on the left side (plate XXXVIII, fig. 16), and running posteriorly, diminishes to a few cells which disappear behind the level of the 18th somite. It is noteworthy that posterior to the mid-region of the 14th somite on the left side a definite outgrowth was observed, extending out from the vesicle towards the duct, but failing to reach the latter. The region, therefore, which gives rise to the Wolffian duct, certainly does not extend posteriorly beyond the mid-region of the 14th somite, and very possibly not beyond the 13th somite.

The coelomic vesicles are well marked, three being present opposite the 11th, 12th, and 13th somites (plate XXXVII, fig. 14, plate XXXVIII, fig. 15, *ves.*), and two opposite each succeeding one up to the 16th, where they become less distinct, continuing back into a thickened area of the somitic stalk, which soon becomes solid, and which can be followed to the hinder end as a slightly swollen region of the mesoderm lying immediately adjacent to the coelom. Each vesicle is connected with the coelomic epithelium (plate XXXVIII, fig. 16, *con.*) by a solid mass of cells, opposite which a groove may be present.

In embryos with 20 somites, the vesicles opposite the 16th and 17th somites are already united with the Wolffian duct, the latter extending a short distance behind the 20th somite. Plate XXXVIII, fig. 17 shows the duct (*ex.d.*) near its posterior end in an embryo of 21 somites, lying in an indentation in the ectoderm. In some cases, as was observed in embryos of 22 to 23 somites, solid sprouts appear to grow out from the ventro-lateral wall of the duct towards

the vesicle, although more usually, the union between the two is effected by outgrowths from the dorso-lateral wall of the vesicle towards the duct.

Later stages. In succeeding stages the pronephric ridge disappears opposite the 8th somite, whilst in the region of the 9th, 10th, and cranial part of the 11th somites small tubular remnants are found, sometimes connected with the coelomic epithelium by a few cells. Behind this level definite mesonephric tubules are developed, although they are only small and vestigial opposite the 11th somite. In embryos of 27 somites for example, three or four are developing opposite the 11th somite, three opposite the 12th and 13th (plate XXXVIII, fig. 18), two or three opposite the 14th, and two opposite each succeeding somite; each is connected with the coelomic epithelium by a short solid band of cells, these bands being more distinct at some places than at others.



TEXT-FIG. 2. Embryo with 45 somites. Transverse section (composite) through the external glomerulus (*ext.gl.*) and first excretory tubule (*t*) in the region of the 9th somite and 6th spinal ganglion. Left side. *a* = aorta. *cd.* = degenerate cord of cells connecting the tubule with the glomerulus. *pc.* = posterior cardinal vein. *W.D.* = Wolffian duct.

(Sl. 5–5–4 to 7)

From the 18th somite backwards the vesicles are no longer united with the excretory duct; they gradually run into each other and their central cavities become reduced. The duct reaches the wall of the cloaca about this stage, and actually opens into the latter in embryos with 36 to 37 somites.

The mesonephric tubules are formed in the typical manner. The vesicle becomes flattened and invaginated, and develops into the Malpighian body, whilst the connection between the latter and the Wolffian duct becomes elongated and coiled to form the tubule. Definite glomeruli first appear in embryos with 35 to 36 somites, from the region of the 12th somite posteriorly; small and very rudimentary glomeruli may develop, opposite the end of the 11th somite, but these always remain vestigial. Plate XXXVIII, fig. 19, shows a well marked glomerulus developing in the region of the 12th somite in the embryo with 35 to 36 somites. At this stage the first somite is very small but apparently has not yet disappeared.

The primordium of the ureter first appears in an embryo of 38 to 39 somites as a slight dilatation on the dorsal side of the excretory duct, some distance behind the last tubule. At this stage, excluding about five tubular remnants at the anterior end, there are altogether 43 tubules on the left side, the last four not yet united with the duct. In an embryo with 50 to 51 somites, where the distal end of the ureter is expanding into the thick walled pelvis, surrounded by a dense layer of mesenchyme, about 50 tubules were counted; of these, one or two at the cranial end possessed only rudimentary glomeruli, whilst two or three glomeruli at the posterior end were very small and poorly developed. At one stage with 45 somites a very small but definite external glomerulus was present on a level with the first degenerate tubule of the left side, in the region of the 9th somite and the 6th spinal ganglion. A solid degenerate cord of cells connected the distal end of the tubule with the glomerulus (text-fig. 2, *ext.gl.*). In no other embryo was an external glomerulus observed.

In the oldest stage examined (about 55 somites) the Malpighian capsules were still connected with the coelomic epithelium either by strands of cells, or, more rarely, by a diffuse cellular mass.

SUMMARY AND DISCUSSION

The cranial end of the excretory system in the cat is first developed in the form of a continuous ridge, the pronephric ridge, which arises as a thickening of the somatic layer of the intermediate cell mass or somitic stalk uniting the somite with the lateral plate. This thickening, which first appears in embryos with 8 to 9 somites, begins in the region of the 7th somite and increases gradually in thickness from before backwards to the level of the 13th or 14th somite. During the same time as the formation of the ridge, in embryos with 9 to 17 somites, a series of coelomic chambers becomes cut off from the general body cavity. They are very poorly developed anteriorly, but from the 9th somite backwards to the region of the shortened primitive streak, they form a well marked series one behind the other, being most conspicuous in the embryo of 12 somites. I have suggested that these structures represent vestigial pronephric chambers. When best developed (plate XXXV, fig. 5), each forms a well defined chamber lying immediately ventro-laterally to the pronephric ridge and communicating with the general body cavity by a narrow passage, the peritoneal funnel. In older embryos the coelomic chambers disappear completely in front of the 10th somite, probably becoming once more a part of the general coelom, but from this level down to the posterior end, they appear to become closed off from the coelom, and come to form a longitudinal cord of tissue, roughly circular in cross section, the entire cord being connected throughout its length with the coelomic epithelium by a short solid band of cells, representing the united and now closed peritoneal funnels. The cavities of the chambers become very much reduced in the anterior

portion from the 11th to the 14th somites but apparently never quite disappear, but behind this level they become completely obliterated. Very soon, however, cavities again appear, and the whole structure becomes divided up into a series of vesicles. three opposite each of the somites from the 11th to the 14th inclusive and two opposite each succeeding somite as far as the latter are developed, each vesicle being united with the coelomic epithelium by a solid column of cells, opposite which vestiges of a funnel may be present as a groove running inwards from the coelom.

In the region in front of the 11th somite the pronephric ridge has the form of a thickening of the dorsal wall of the somitic stalk, but from the hinder part of the 11th to the 13th or 14th somite, it appears as a thickening on the dorsal side of the longitudinal cord of tissue formed by the closed coelomic chambers, and therefore, at the points where vesicles develop, as a swelling on the wall of each vesicle.

From the pronephric ridge the excretory duct takes its origin. The ridge may be represented by a very slight swelling of the somatic wall of the stalk, consisting of a few cells, opposite the 6th somite, whilst opposite the 7th, it is very small and never contributes towards the formation of the excretory duct, nor are any tubules developed in this region. The rudiment opposite the 8th somite is more definite and may possibly take a small part in the composition of the duct. From this level posteriorly, a small portion becomes split off from the dorsal margin of the ridge at regular intervals, the amount separated off increasing in size from before backwards. The points at which connection is retained later become luminated and constitute the excretory tubules; from the region of the 11th to the 13th somites the tubules develop at the level of the vesicles, the splitting off occurring between the vesicles. Thus the region from the 8th or 9th to the 13th somites gives rise to the Wolffian duct, its main seat of origin being opposite the 11th, 12th, and 13th somites. Behind the 13th somite the duct grows back independently, and its union with the vesicles is a secondary one, occurring either as a solid outgrowth from the dorso-lateral wall of the vesicle towards the duct, or apparently sometimes as an outgrowth of the ventro-lateral wall of the duct towards the vesicle. It must be noted, however, that opposite the 14th somite a vesicle may be found to be united with the duct before the latter has begun to grow freely backwards, as in one embryo of 19 somites, so that the region from which the duct arises may extend as far as the 14th somite, and possibly varies in different embryos. In any case, at this level and also opposite somite 15, the union of the vesicles with the duct occurs very early; moreover, as will be seen from the subsequent discussion, the exact point from which the duct begins its independent growth is probably not of great morphological importance.

Unfortunately, the exact mode of origin of the anterior portion of the duct was not determined with certainty. In one embryo, that of 14 somites, a definite but very short outgrowth from the ridge is present at the level of the 10th somite; this extends dorsally and posteriorly, its hinder tapering end,

which consists of only two cells, uniting once more with the ridge. Posterior to this level, however, the duct appears simply to become split off from the ridge between the points at which tubules arise, and all signs of metamerism are absent from the first. Whether the condition opposite somite 10 is the normal one, and whether it represents a segmental outgrowth, it was not possible to decide without more embryos of this age. Definite segmental outgrowths, which unite to form the pronephric duct, have been described in the rabbit and mole by Kerens ('07) and at the cranial end in man by Felix ('12). They may possibly occur in the cat opposite the 8th and 9th somites as well as the 10th, but in this mammal the anterior end of the organ is very degenerate, and if a stage of definite segmental outgrowths is present, it is passed through with great rapidity, and could only be observed by the careful examination of many embryos of the same age.

The excretory duct when first formed is solid or possesses a latent lumen, and appears as a mass of cells lying dorsally to the pronephric ridge and just above the vesicles posteriorly to the ridge. Its posterior free tip consists of a fine cellular strand almost embedded in the ectoderm and sometimes almost indistinguishable from it. There is, however, no definite evidence that the ectoderm takes a part in the formation of the duct. Soon a distinct cavity appears within it, and it reaches the ventro-lateral wall of the cloaca in embryos with 27 to 29 somites, actually opening into the latter in stages with 36 to 37 somites.

The anterior end of the excretory organ in the cat is obviously undergoing atrophy. Opposite the 6th and 7th somites degeneration is almost complete, and neither in this region nor opposite somite 8 are any tubules developed. Isolated tubular remnants are present opposite the 9th somite, and posterior to this level they gradually become larger and more definite. They are still rudimentary and few in number opposite the 10th and beginning of the 11th somite, but towards the hinder region of the latter they increase in size and the first internal glomeruli are apparent, although here the latter are always very small and quite vestigial, the anterior end of the functional mesonephros lying in the region of the 12th somite.

The pronephric region in both reptiles and mammals is usually regarded as that region from which the excretory or Wolffian duct arises. That this distinction has no value is shown by Brauer in the Gymnophionan Hypogeophis. Here the pronephros is probably as well developed as in any other vertebrate, except perhaps the Myxinoids, and stretches from the 4th to the 15th segments; twelve pronephric canals are laid down but only the first three of these form the pronephric duct. The level at which the excretory duct becomes independent does not therefore necessarily mark the hinder limit of the pronephros. According to Kerens ('07), the duct takes its origin in the mole from three tubules arising opposite the 8th, 9th, and 10th somites, whilst in the rabbit an extra one is developed opposite the 7th somite. These tubules, which are thus strictly segmental, are all small and atrophy early. Posteriorly to the

10th somite the last tubule passes back into a cellular cord which becomes entirely separated from the lateral plate.

In the marmot as described by Janosik ('04), the dorsal portions of the "middle plate," connecting the somite with the lateral plate, from the distal end of the 6th to the 12th somites, give rise to a cell mass which eventually forms a cell strand, the latter growing distally as the Wolffian duct. The strand remains connected with the coelomic epithelium at intervals by rudimentary canals, six or seven being present. From the level of the 13th somite to the 15th or 16th, the duct is split off as a whole from the dorsal side of the middle plate, and posterior to this region it grows back independently. The cranial portion, as far as the level of the 12th somite, is regarded as homologous with the pronephros, and that between the 12th and 15th or 16th somite is considered as a region of transition between pro- and mesonephros. Here, and posteriorly to the hinder end of the mesonephros, the middle part separates off both from the somite and the coelomic epithelium, forming a cellular cord, which later divides into a species of dysmetameric vesicles. This process strikingly recalls the conditions in the cat. It is worthy of note that the primordium of the mesonephric canals, both in the marmot and the cat, is regarded as a portion cut off from the coelomic epithelium.

In an embryo of the bat, *Rhinolophus hipposideros*, van der Stricht ('13) has described two pronephric vestiges between the 7th and 8th somites, and one between the 9th and 10th on the left side, whilst on the right one is found opposite the 7th somite and two opposite the 8th and 9th.

The pronephros in man, as observed by Felix ('12), extends from the 7th to the 14th segments. Only the three anterior primordia are completely separated from each other and show some metamerism, whilst the hinder tubules are not segmental, altogether six being present opposite the 10th, 11th, and 12th segments. Whether this dysmetamerism is primary or not was not determined owing to want of sufficient material.

In Echidna (Keibel ('03)) vestiges of eight primordia have been observed in the region of the 4th, 5th, and 6th spinal ganglia, behind which typical mesonephric tubules begin, the first glomeruli appearing between the 7th and 8th spinal ganglia, that is presumably between the 10th and 11th somites, at a level only slightly in front of the anterior glomeruli in the cat.

In the marsupial Trichosurus vulpecula (Buchanan and Fraser ('18)) there are a large number (about 14 to 16) of degenerating excretory tubules, beginning opposite the 4th spinal ganglion and extending as far as the 8th, where rudimentary internal glomeruli are developed. As the necessary early stages were missing it was not possible to ascertain how many of these take part in the formation of the excretory duct. In an embryo of Perameles, however, with 15 to 16 somites, the excretory tubules appear to be primarily connected with the duct as far back as the 13th somite, and it is quite possible that this condition also exists in Trichosurus, for it is evident, from our observations on the cat, that the presence of internal glomeruli does not mark the boundary

between so-called pro- and mesonephric tubules, as was supposed in the earlier paper on Trichosurus ('18). In Trichosurus, as in the cat, there was absolutely no evidence of the two kinds of tubules occurring in the same segment.

The mode of origin of the mesonephric tubules in the cat follows that described in other forms. The dorsal wall of each vesicle becomes flattened and then invaginated to form the Malpighian capsule, on the dorsal side of which the glomerulus arises. The solid connection between the vesicle and the Wolffian duct soon becomes tubular and coiled, and eventually develops into the secretory and excretory parts of the organ. The vesicles extending from the level of the hinder end of the 11th to the 13th somites, from which the duct takes its origin, give rise to tubules which are serially homologous with those behind this region; all are typical mesonephric tubules. That being so, the distinction in the cat between pronephric and mesonephric regions is purely arbitrary, for no definite line can be drawn between the two areas. The whole excretory organ must be looked upon as one continuous organ, the anterior portion of which shows progressive deterioration from behind forwards.

The view that pro- and mesonephros are different parts of the same organ was first put forward by Balfour and Sedgwick ('79), was later supported by Renson ('83) and Weldon ('83), and has since been upheld by several recent investigators [Wiedersheim ('90) in reptiles, Field ('91) in Amphibia, Price ('97 and '04) in Myxinoids, Brauer ('02) in the Gymnophiona, Kerens ('07) in Reptilia, Aves and Mammalia, Burland ('13) in Chelonia, and Borcea ('05) in Elasmobranchii]. More recently Graham Kerr ('19) has supported the same theory in his text book on the embryology of Fishes and Sauropsida. Many observers [Rückert ('88), van Wijhe ('89) and Rabl ('96) in Selachii, Semon ('92) in Ichthyophis, Hoffmann ('89) in Lacerta, Felix ('91) in the chick, Maas ('97) in Myxine, Wheeler ('99) and Hatta ('00) in Petromyzon, Gregory ('09) in the Turtle] regard the pronephros as having once extended all down the body, but as having later undergone atrophy, being replaced, except in the cranial region, by another series of tubules forming the mesonephros. These authors contend that both pro- and mesonephric canals may develop in the same segments, the mesonephric primordia arising from a more dorsal part of the somitic stalk than the pronephric. It must be said, however, that the figures given to illustrate so-called mesonephric primordia in the pronephric region are quite unconvincing.

It seems very probable, as Brauer ('02) suggests, that the canal-like connection between the somite and the nephrotome, seen in the last stage of separation between the two, has in some instances, been mistaken for a mesonephric canal. In the cat, the portion of the somitic stalk connecting the hinder end of the somite with the pronephric ridge often contains a distinct central cavity, forming, in cross section, a vesicular region of the stalk. This is especially well marked in embryos with 19 somites (plate XXXVIII, fig. 20, *s.q.*), but later completely disappears. In the cat, however, such structures have

no connection whatever with the mesonephric vesicles, which arise laterally to the pronephric ridge.

Borcea ('05), in his studies on Elasmobranchii, also considers that the mesonephric canals arise from a more dorsal part of the nephrotome than the pronephric, but that the limits between the two cannot be definitely determined, and he holds at the same time that pro- and mesonephros are parts of one organ, at first similar, but later undergoing physiological differentiation in two directions. This difference in function has led to a difference in development (Borcea, p. 340).

That the external glomeruli of the pronephros are homodynamous with the internal glomeruli of the mesonephros, the one gradually passing into the other, has been pointed out by Sedgwick ('81), also by Renson ('83) and Mihalkovics ('85), although the latter worker did not consider the homology between the two excretory organs a complete one. Many of the later workers also look upon the Malpighian capsules simply as pronephric chambers or nephrotomes, which have become completely closed off from the body cavity, the external glomerulus thus becoming internal. This view is upheld by Wiedersheim ('90) and Burland ('13) in Reptilia, Field ('91) in Amphibia, Price ('97) in Myxinoidei, Brauer ('02) in Hypogeophis, and Borcea ('05) in Elasmobranchii. The similarity of the two structures is illustrated in Lepidosteus (Balfour and Parker ('82) and Beard ('94)) where the glomerulus of the pronephros lies in a chamber which is cut off from the body cavity, and which is identical with a Malpighian capsule. According to Price, who has investigated Bdellostoma, the homology between the two is a very complete one. In the Mammalia this homology has not been demonstrated, the rudimentary state of the anterior end of the excretory organ and the absence of external glomeruli, except in a very degenerate condition, making a comparison between the latter and the internal glomeruli of the mesonephros almost impossible. In early embryos of the cat there is a series of coelomic chambers extending from the 6th somite to the hinder end of the body. Such structures do not appear to have been previously described in a mammal; they are, however, quite definite in the cat, and it has been suggested that they are equivalent to vestigial pronephric chambers. They are especially well developed in the embryo with 12 somites, but they very soon undergo a change, and from the region of the 11th somite backwards, close off from the coelom and come to form an almost solid cord (corresponding with a nephrogenic cord), attached throughout its length to the coelomic epithelium. This cord later divides up into a series of vesicles, the central cavity in each of which, behind the level of the 13th somite, arises secondarily. Each vesicle remains united with the coelomic epithelium by a solid mass of cells. Though it is difficult to demonstrate conclusively that the longitudinal cord of tissue, in which the vesicles arise, is actually derived from the pronephric chambers, this interpretation seems to be the correct one. If so, then the pronephric chambers are homologous with the Malpighian capsules.

The connections of the vesicles with the coelomic epithelium, representing the closed peritoneal funnels, persist for a considerable period. When the Malpighian body is developed, its ventral wall is seen to be connected with the coelomic epithelium either by a more or less definite cord of cells, or by a diffuse mass of mesenchyme, similar to that described in the marsupial Perameles (Fraser, '19). In the cat, these atrophied funnels are still present in an embryo with about 55 somites, but as I have not yet studied older stages, it is not possible to say whether or not they are transformed directly into the rete tubules as in the case of Perameles. The development of the vasa efferentia has, however, been studied by Sainmont ('06). This author states that the rete first appears in embryos of 24 days, when it arises as outgrowths from the walls of the Malpighian capsules. It is not unusual for the peritoneal connection of the mesonephric tubules to be lost and regained, a secondary union arising as an outgrowth from Bowman's capsule towards the coelomic epithelium, and developing finally into a definite open peritoneal funnel. This condition is found, for example, in Hypogeophis (Brauer, '02) and also in Amphibia (Fürbringer '78). That great variation exists is evident from the divergence of opinion expressed by so many observers, not only in different vertebrates but in one and the same species, some attributing the origin of the rete to outgrowths of the Malpighian bodies, others to evaginations of the peritoneal epithelium, and yet others to a condensation of mesenchyme lying between the peritoneum and Bowman's capsules. Many workers, again, experience great difficulty in distinguishing the exact origin of the cells from which the rete is derived.

In conclusion, it may be said that the anterior region of the excretory system in the cat is as well developed as in other mammals, with the probable exception of the Marsupialia and the Monotremata. The number of rudimentary tubules, although slightly in excess of man, is apparently less than in marsupials. The cranial end is undergoing atrophy as in all mammals, and whilst the incompletely formed tubules in front of the 11th somite may possibly have a segmental origin, behind this level all signs of metamerism have disappeared. Vestigial external glomeruli may develop in later stages (e.g. 45 somites) but only rarely; such structures have been described in man, and in the marsupial Trichosurus, but in the rabbit, mole, and marmot they appear to be completely absent. The whole excretory system is composed of one continuous series of tubules, the structure of which increases in complexity in an antero-posterior direction, there being no clear distinction between the anterior tubules ordinarily regarded as forming the pronephros, and the posterior tubules of the mesonephros.

CONCLUSIONS

The embryonic excretory system in the cat is one continuous organ, the degenerate anterior end passing posteriorly into the fully developed mesonephros.

In early stages an intermediate cell mass or somitic stalk connects the mesoblastic somite with the lateral plate.

A pronephric ridge is developed as a thickening of the somatic wall of the intermediate cell mass. This ridge extends from the level of the 6th to the 13th or 14th somite increasing in thickness from before backwards. The hinder portion, from the region of the 9th somite posteriorly gives origin to the excretory or Wolffian duct.

During the formation of the pronephric ridge and immediately laterally to it, a series of coelomic chambers become cut off from the general body cavity communicating with the latter by a narrow passage. These extend from about the level of the 6th somite almost to the posterior end of the embryo. It is suggested that they represent vestigial pronephric chambers, each with a peritoneal funnel.

The chambers in front of the 11th somite soon disappear, but behind this region it appears as if they become completely closed off from the body cavity so as to form an almost solid longitudinal cord of tissue, attached throughout its length to the coelomic epithelium by a solid band of cells, representing the closed peritoneal funnels.

Later this cord becomes divided into a series of vesicles each united to the coelomic epithelium by a cord of cells. In the region from about the 11th to the end of the 13th somite the cavities of the coelomic chambers become reduced but nevertheless persist, but posteriorly the vesicles arise secondarily within the cord. There are three vesicles opposite the 11th to the 14th somites, and two opposite each somite posteriorly.

The greater part of the Wolffian duct arises in the region of the 11th to the 13th somites. It becomes split off from the dorsal margin of the ridge between the vesicles, connection being retained opposite the latter where tubules later arise. In front of the 11th somite definite segmental outgrowths may possibly occur from the ridge, the distal ends of which unite to form the anterior end of the excretory duct.

Behind the level of the 13th or 14th somite the duct grows back independently, its free tip lying in an indentation of the ectoderm. There is no direct evidence that the ectoderm takes a part in its formation.

The Wolffian duct reaches the wall of the cloaca in embryos with 29 somites and opens into the latter in embryos with 36 to 37 somites.

From the 11th to the 13th somites the connection of the vesicles with the Wolffian duct is thus primary, behind this level the union is a secondary one.

Each vesicle develops into the Malpighian body of a mesonephric tubule and the connection between the vesicle and the duct becomes the excretory tubule.

Definite mesonephric tubules are present from the level of the hinder end of the 11th somite posteriorly, though the glomeruli at the extreme anterior end are quite rudimentary. In front of this level only vestigial tubules are developed.

An external glomerulus was observed in only one embryo with 45 somites in the region of the 9th somite and the 6th spinal ganglion.

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a = dorsal aorta; *b.c.* = body cavity; *c.ch.* = coelomic chamber; *ect.* = ectoderm; *ent.* = entoderm; *ex.d.* = excretory duct; *m.p.* = medullary plate; *n.* = notochord; *n.t.* = neural tube; *p.f.* = peritoneal funnel; *p.r.* = pronephric ridge; *S*1, 2, ... = somite 1, 2, ... ; *smpl.* = somatopleure; *spl.* = splanchnopleure; *ves.* = coelomic vesicle.

DESCRIPTION OF PLATES

The figures are reproduced at a magnification of 200 diam.

Fig. 1 *a*. Embryo with 9 to 10 somites. Transverse section at the level of the 8th somite, showing the somitic stalk or intermediate cell mass at the point where it is isolated from the somite. Left side. (Sl. 2–6–14.)

Fig. 1 *b*. Embryo with 9 to 10 somites. ·01 mm. behind *a*, showing the thickening of the dorsal wall (*p.r.*) of the somitic stalk. (Sl. 2–6–15.)

Fig. 2. Embryo with 9 to 10 somites. Transverse section at the level of the 9th somite on the left side, showing the coelomic chamber (*c.ch.*) and thickening of the somitic stalk. The latter in this section is not united with the somite. (Sl. 2–7–8.)

Fig. 3. Embryo with 9 to 10 somites. Transverse section at the level of the 10th somite, showing the thickening of the somitic stalk (*p.r.*). (Sl. 2–7–16.)

Fig. 4. Embryo with 12 somites. Transverse section through the hinder end of the 8th somite, showing the mid-region of the somitic stalk, which is attached to the lateral plate and disconnected from the somite. Left side. (Sl. 2–1–14.)

Fig. 5. Embryo with 12 somites. Transverse section at the level of the 10th somite, showing the well developed coelomic chamber (*c.ch.*) and the pronephric ridge (*p.r.*). The peritoneal funnel does not appear in this section. Left side. (Sl. 2–3–11.)

Fig. 6 *a* and *b*. Embryo with 12 somites. Two consecutive transverse sections at the level of the 11th somite, showing the pronephric ridge (*p.r.*) and the coelomic chamber (*c.ch.*) with its peritoneal funnel (*p.f.*). Left side. (Sl. 2–4–10 and 11.)

Fig. 7 *a* and *b*. Embryo with 12 somites. Two consecutive transverse sections in the region of the shortened primitive streak, showing a coelomic chamber (*c.ch.*) with its peritoneal funnel (*p f.*). Left side. (Sl. 3–3–10 and 11.)

Fig. 8. Embryo with 14 somites. Transverse section at the level of the 13th somite, showing the pronephric ridge (*p.r.*) and the thickened region of the somitic stalk (*th.*) derived in all probability from a closed coelomic chamber. Right side. (Sl. 3–4–7.)

Fig. 9. Embryo with 17 somites. Transverse section at the level of the 10th somite, showing the separation of the excretory duct (*ex.d.*) from the dorsal margin of the pronephric ridge (*p.r.*). Left side. (Sl. 4–3–8.)

Fig. 10. Embryo with 17 somites. Transverse section showing the pronephric ridge (*p.r.*) at the level of the 10th somite. Right side. (Sl. 4–3–9.)

Fig. 11. Embryo with 17 somites. Transverse section showing the pronephric ridge at the level of the 11th somite. Right side. (Sl. 4–5–7.)

Fig. 12. Embryo with 17 somites. Transverse section at the level of the anterior end of the 13th somite, through the anterior wall of a vesicle (*ves.*), and showing the last vestige of the peri toneal funnel (*p.f.*). The excretory duct (*ex.d.*) lies free above the vesicle. Right side. (Sl. 5–2–3.)

Fig. 13. Embryo with 17 somites. Transverse section, ·03 mm. posterior to fig. 12, showing the central cavity within the vesicle, and the free excretory duct (*ex.d.*) above the latter. (Sl. 5–2–6.)

Fig. 14. Embryo with 19 somites. Transverse section in the region of the 12th somite, showing the pronephric ridge (*p.r.*) forming a thickening of the dorsal wall of the vesicle (*ves.*). (Sl. 1–7–15.)

Fig. 15. Embryo with 19 somites. Transverse section at the level of the 13th somite, showing the free excretory duct lying immediately dorsally to a vesicle, and a short distance behind its last connection with the pronephric ridge. Left side. (Sl. 4–5–10.)

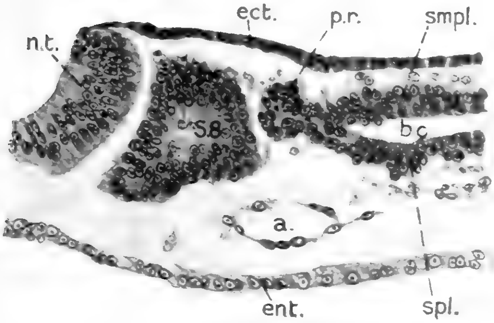
Fig. 16. Embryo with 19 somites. Transverse section between the 14th and 15th somites, showing the solid connection (*con.*) of a vesicle with the coelomic epithelium. The now luminated excretory duct is seen lying dorsally to the vesicle. Left side. (Sl. 1–9–6.)

Fig. 17. Embryo with 21 somites. Transverse section showing the excretory duct (*ex.d.*) near its hinder end lying in an indentation of the ectoderm. *s.mes.* = somitic mesoderm. (Sl. 7–4–5.)

Fig. 18. Embryo with 27 somites. Transverse section through a developing mesonephric tubule at the level of the 13th somite. Right side. *M.c.* = future Malpighian capsule. (Sl. 2–1–17.)

Fig. 19. Embryo with 35 to 36 somites. Transverse section at the level of the 12th somite and 9th spinal ganglion, showing an excretory tubule (*ex.t.*) with its developing glomerulus (*gl.*). Left side. (Sl. 3–4–5.)

Fig. 20. Embryo with 19 somites. Transverse section between the 9th and 10th somites, showing the vesicular region (*S.* 9) of the somitic stalk connecting the hinder end of the 9th somite with the pronephric ridge (*p.r.*). Right side. (Sl. 1–5–9.)



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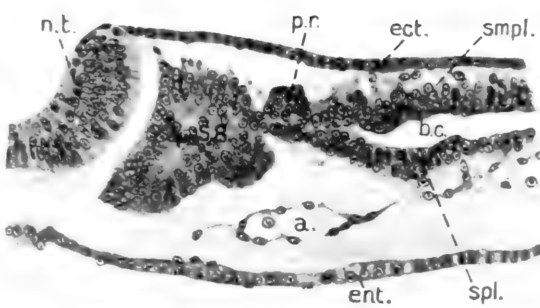

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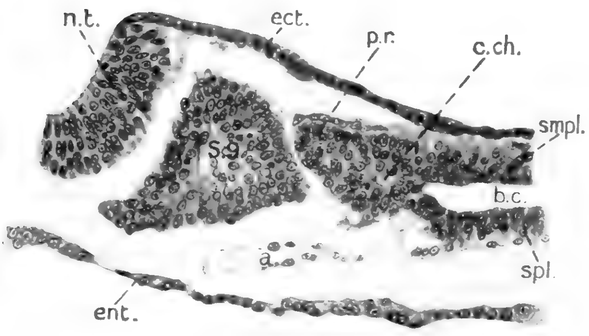
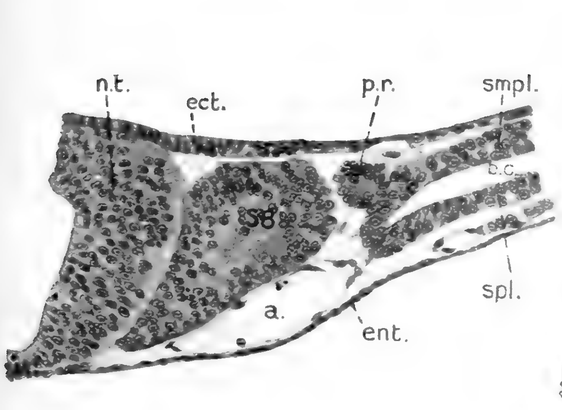


Fig. 2.



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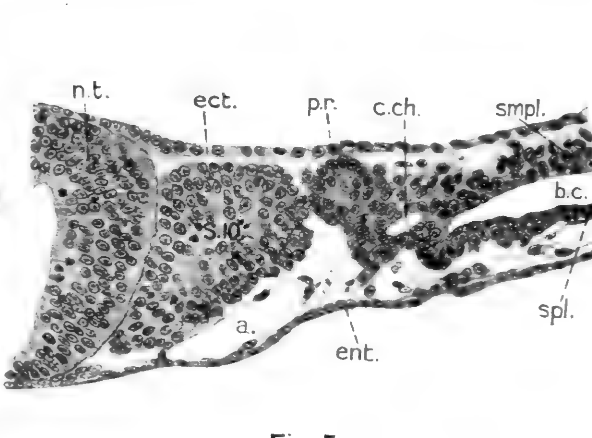

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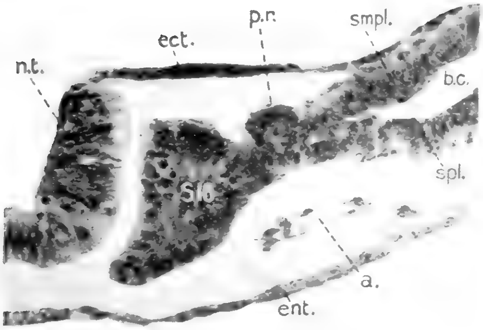

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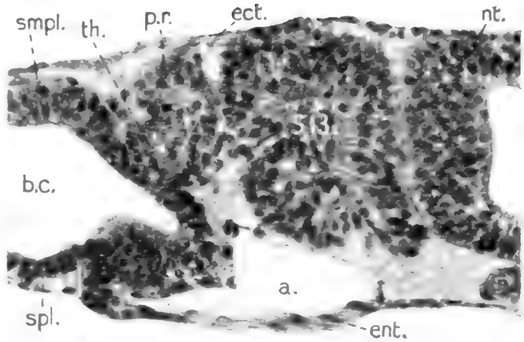

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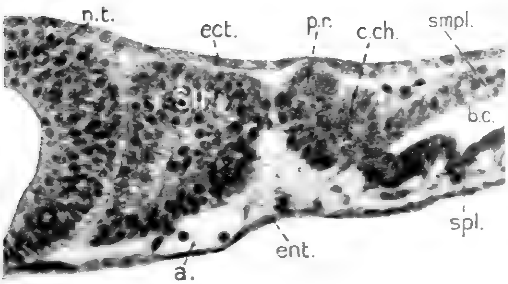
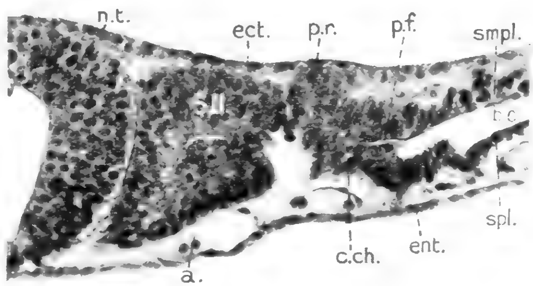


Fig. 6a.



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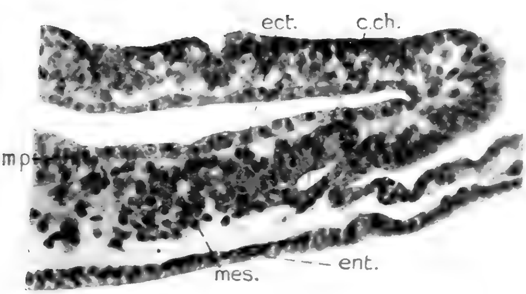

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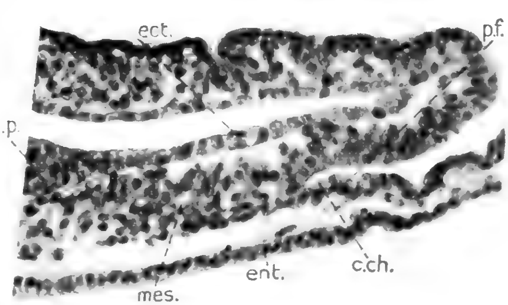

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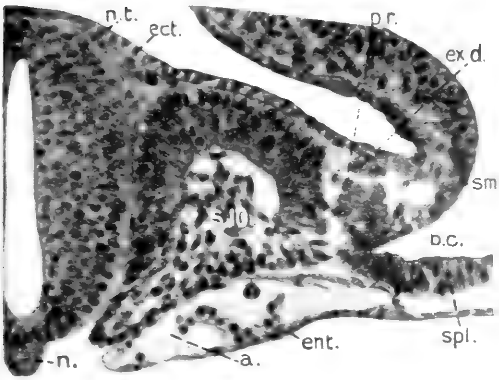

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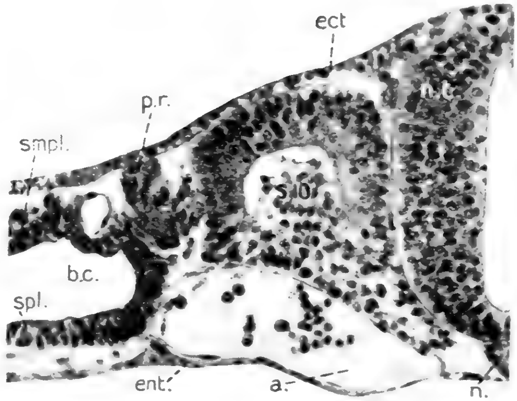

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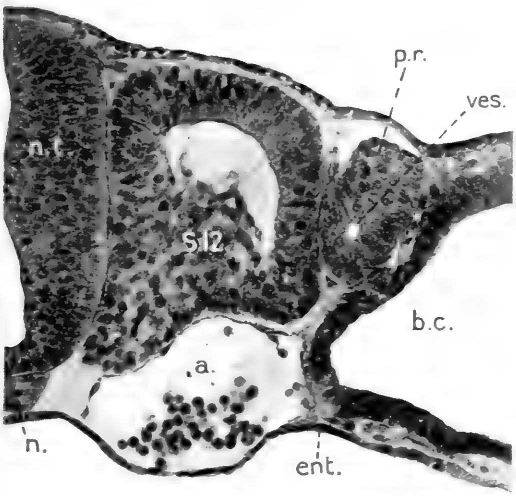

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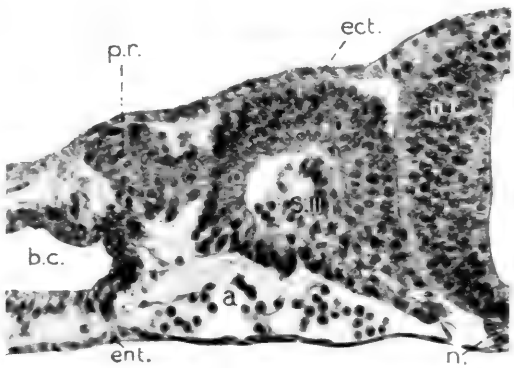
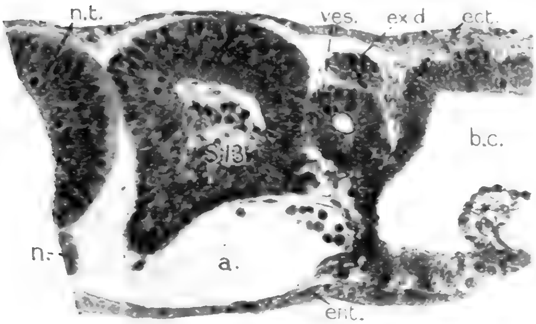


Fig. 11.

Fig. 12.

Fig. 13.



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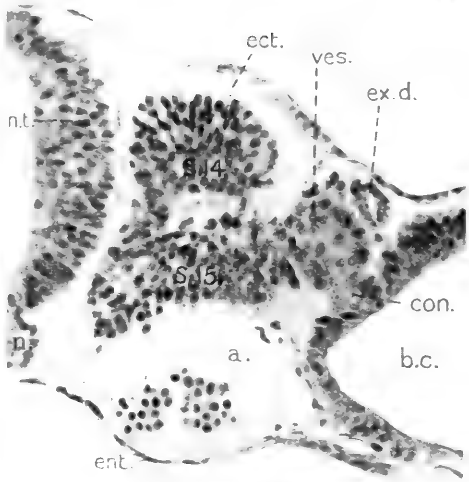

Fig. 16.

Fig. 18.

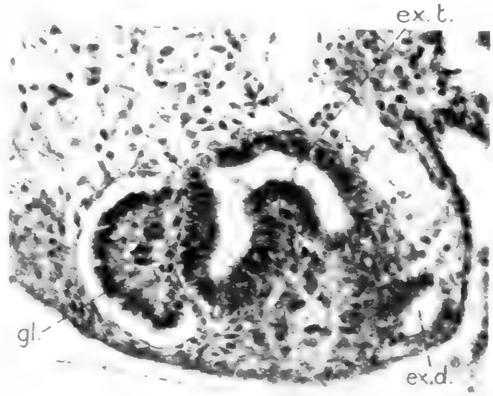

Fig. 19.

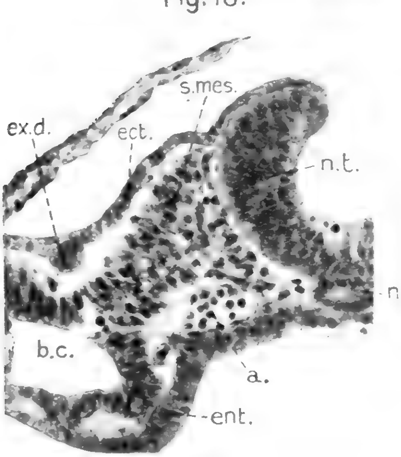

Fig. 17.

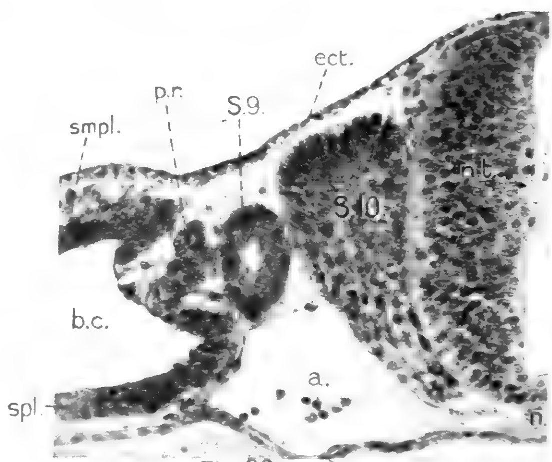

Fig. 20.

ON CERTAIN ABSOLUTE AND RELATIVE MEASUREMENTS OF HUMAN VERTEBRAE

By EDGAR F. CYRIAX, M.D. (Edin.),
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Some years ago Anderson[1] and Dwight[2] made a series of measurements of certain diameters of human vertebrae, namely the anterior vertical, posterior vertical, transverse and antero-posterior of the body and the transverse of the whole bone. Their results agreed very closely in most cases. Neither of these authors however appear to have measured the antero-posterior diameter of the whole vertebra nor to have attempted to ascertain whether any constant ratios existed between the various measurements obtained. It seemed to me that such an investigation might prove of interest, partly from the purely anatomical and anthropological aspect, partly from the view of interpretation of skiagrams and correct estimation of spinal deformities, and possibly also from the medico-legal point of view.

I accordingly made a series of measurements of (as far as could be ascertained) normal human vertebrae taken from 36 articulated and disarticulated skeletons and spinal columns, 9 dry preparations of vertebral war injuries and about 600 loose vertebrae: in all 1482 bones were thus examined. The actual measurements taken were as follows:

(1) The mesial anterior vertical diameter of the body.

(2) The lateral diameter of the body. In the cervical region this was measured just above its lower margin, in the dorsal and lumbar at the middle of the body, thus obtaining its minimum lateral diameter.

(3) The maximum diameter of the whole vertebra, i.e. the spread of the transverse processes.

(4) The maximum antero-posterior diameter of the whole vertebra. This was measured from the centre of the lower margin of the body to the most distant point on the spinous process.

For the sake of brevity these diameters will be referred to as: body, A.V.D.; body, L.D.; T.D. and A-P.D.

From the measurements thus obtained, the following ratios were then calculated:

(*a*) Body A.V.D. to T.D.
(*b*) Body A.V.D. to A-P.D.
(*c*) Body L.D. to T.D.
(*d*) Body L.D. to A-P.D.
(*e*) T.D. to A-P.D.

[1] *Journ. of Anat. and Phys.* 1883, XVII. 341–344.
[2] Quoted Piersol, *Human Anatomy*, 1908, p. 122.

I found that although individual characteristics are quite constant, very great variations occurred in both measurements and ratios, specially the latter, 60 per cent. being quite common, and 100 per cent. being reached in a few cases. As examples I give the results obtained from the first six specimens examined in the following three vertebrae:

Fifth cervical.

	mm.	mm.	mm.	mm.	mm.	mm.
(*a*) Body A.V.D. ...	15	9	13	13	11	13
(*b*) Body L.D.	24·5	24	24	22	20	18·5
(*c*) T.D.	59	58	61·5	58·5	48	50·5
(*d*) A-P.D.	46·5	47	51	48·5	45·5	41·5
	%	%	%	%	%	%
Ratio of (*a*) to (*c*) ...	25	16	21	22	23	26
,, (*a*) to (*d*) ...	32	19	25	27	24	31
,, (*b*) to (*c*) ...	42	41	39	38	42	37
,, (*b*) to (*d*) ...	53	51	47	45	44	45
,, (*c*) to (*d*) ...	127	123	121	121	105	122

Sixth dorsal.

	mm.	mm.	mm.	mm.	mm.	mm.
(*a*) Body A.V.D. ...	19	19	19	21	20	21
(*b*) Body L.D.	23	23·5	27	30·5	31	29
(*c*) T.D.	54·5	54	63·5	68	67·5	68·5
(*d*) A-P.D.	59	62	70	77	72·5	75
	%	%	%	%	%	%
Ratio of (*a*) to (*c*) ...	35	35	30	31	30	31
,, (*a*) to (*d*) ...	32	31	27	27	28	28
,, (*b*) to (*c*) ...	42	44	42	45	46	42
,, (*b*) to (*d*) ...	39	38	39	40	43	39
,, (*c*) to (*d*) ...	91	87	91	88	93	91

Third lumbar.

	mm.	mm.	mm.	mm.	mm.	mm.
(*a*) Body A.V.D. ...	30	24	24	27	30	28
(*b*) Body L.D.	45	42·5	44	41	39	31·5
(*c*) T.D.	108	83	82	98	79	76·5
(*d*) A-P.D.	85	77	85	86·5	76	70·5
	%	%	%	%	%	%
Ratio of (*a*) to (*c*) ...	28	29	29	28	38	37
,, (*a*) to (*d*) ...	35	31	28	31	39	40
,, (*b*) to (*c*) ...	42	51	54	42	49	41
,, (*b*) to (*d*) ...	53	55	52	47	51	45
,, (*c*) to (*d*) ...	127	108	96	113	104	109

The summary of the measurements (calculated to the nearest whole number) and ratios are given below. I have not made separate summaries of male and female bones respectively because in all but a very few cases it was impossible to be certain that any given skeleton consisted entirely of the bones of purely one individual; moreover I was informed that the makers of articulated skeletons occasionally join male spinal columns to female pelves

Summary of diameters.

	No. of specimens examined	Body A.V.D. Average mm.	Min.	Max.	Body L.D. Average mm.	Min.	Max.	T.D. Average mm.	Min.	Max.	A-P.D. Average mm.	Min.	Max.
C 1	152	—	—	—	—	—	—	78·07	63	90	45·41	39	53
C 2	157	39·22	30	49	—	—	—	54·49	44	65	50·59	43	58
C 3	42	12·85	10	16	20·94	14	25	53·48	44	60	44·92	39	54
C 4	37	12·55	7	15	21·30	17	25	55·07	47	61	45·07	39	54
C 5	38	12·16	9	16	22·58	18	25	57·04	48	64	47·67	41	61
C 6	38	12·07	7	15	25·28	19	29	58·50	50	66	52·21	44	62
C 7	98	13·44	10	17	29·24	23	36	67·95	59	80	58·75	51	70
D 1	110	15·45	12	19	30·40	22	37	74·71	57	89	61·24	52	71
D 2	40	17·06	13	21	31·17	20	37	72·54	58	80	65·69	53	72
D 3	37	17·22	13	22	29·48	23	36	65·53	54	78	64·72	54	73
D 4	37	17·78	15	22	27·30	22	32	63·04	52	74	65·72	55	76
D 5	36	18·06	12	21	27·68	22	30	63·35	51	69	66·64	56	79
D 6	35	18·34	15	22	27·77	22	33	63·58	54	69	67·83	58	77
D 7	36	18·75	13	22	28·64	23	34	64·39	54	77	69·63	58	80
D 8	36	19·18	16	23	30·42	24	35	62·49	52	70	69·86	60	80
D 9	36	20·28	16	25	32·12	24	38	64·24	52	71	71·43	60	84
D 10	53	21·21	16	26	34·02	26	38	58·49	49	67	70·56	58	81
D 11	95	22·18	16	27	35·83	27	45	53·24	44	66	70·98	58	86
D 12	104	23·15	17	29	37·97	30	50	47·86	38	63	73·21	61	89
L 1	38	24·38	19	29	39·17	28	44	72·55	58	88	78·58	65	87
L 2	39	25·53	20	32	41·14	28	45	80·23	64	93	81·94	69	92
L 3	38	26·64	21	32	42·79	31	51	89·05	69	108	83·54	70	95
L 4	37	26·78	21	32	44·89	35	53	83·62	63	102	82·30	69	94
L 5	113	27·81	23	34	47·97	39	58	86·00	68	108	76·53	61	96

Summary of relations of diameters.

	Body A.V.D. to T.D. Average %	Min.	Max.	Body A.V.D. to A-P.D. Average %	Min.	Max.	Body L.D. to T.D. Average %	Min.	Max.	Body L.D. to A-P.D. Average %	Min.	Max.	T.D. to A-P.D. Average %	Min.	Max.
C 1	—	—	—	—	—	—	—	—	—	—	—	—	172	144	195
C 2	71	58	89	79	62	95	—	—	—	—	—	—	107	92	129
C 3	24	18	30	29	22	37	39	32	47	47	35	56	119	109	132
C 4	23	15	27	28	17	34	39	33	48	47	41	56	122	102	145
C 5	21	16	27	26	19	32	40	35	49	47	37	55	120	98	140
C 6	21	14	24	23	15	30	43	35	57	48	39	61	112	95	136
C 7	20	15	25	23	18	28	43	33	53	50	42	61	116	98	135
D 1	21	16	28	25	20	32	41	34	49	48	40	62	122	97	142
D 2	25	19	29	27	21	32	43	33	51	47	36	56	114	100	126
D 3	26	22	35	27	22	32	45	36	55	46	37	51	101	87	114
D 4	28	23	36	27	24	35	43	38	53	42	34	49	96	80	111
D 5	29	19	37	27	20	33	44	36	48	42	30	47	96	83	110
D 6	29	24	35	27	23	32	45	39	50	41	35	48	94	76	104
D 7	29	22	37	27	20	31	44	32	52	41	30	49	93	68	106
D 8	31	25	39	27	21	35	49	42	56	44	36	50	90	78	103
D 9	33	26	42	28	24	37	52	37	61	45	37	52	87	69	103
D 10	36	30	49	30	25	39	58	48	70	48	41	65	83	70	93
D 11	43	30	55	31	23	43	67	53	92	50	42	60	75	57	90
D 12	49	35	71	32	26	41	79	56	98	52	40	67	63	49	87
L 1	34	25	47	31	25	42	54	45	67	49	43	58	92	79	109
L 2	32	24	45	31	24	43	51	43	59	50	41	57	98	86	116
L 3	30	22	38	32	27	40	48	34	61	51	44	65	107	91	127
L 4	32	24	42	33	27	40	54	43	72	55	46	69	102	84	121
L 5	32	23	51	36	30	46	56	43	65	63	48	77	112	84	144

and *vice versa.* All that can be said with certainty is that the greater number of bones were from male subjects.

Endeavours on my part to work out formulae derived from one or more measurements or ratios, from which to estimate others, were quite unsuccessful.

CONCLUSIONS

My results agreed fairly closely with those of Anderson and Dwight; in many cases they corresponded exactly and in many others differences of only 1 mm. were encountered. The only differences greater than 3 mm. were: 5 mm. as regards the lateral diameters of the bodies of the last two lumbar vertebrae and 5 mm. as regards the transverse diameter of the whole bone in the fifth lumbar vertebra. The reader is referred to the original measurements of the authors mentioned for more detailed comparison.

NOTE ON THE PERSISTENCE OF THE UMBILICAL ARTERIES AS BLINDLY-ENDING TRUNKS OF UNIFORM DIAMETER IN THE INDIAN DOMESTIC GOAT

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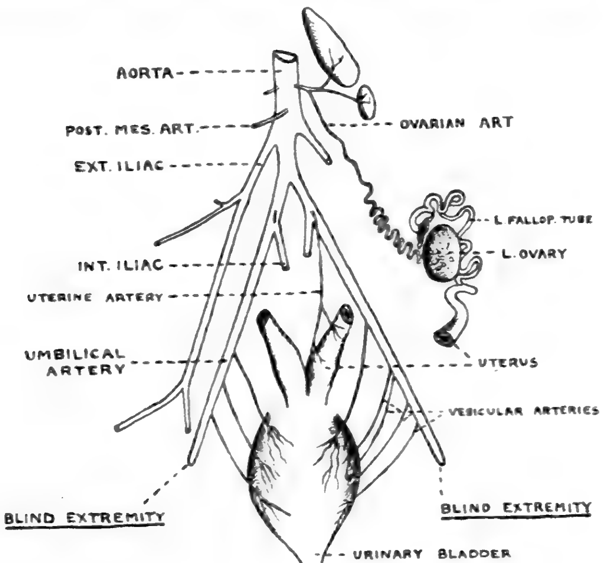
MY attention was first drawn to this peculiar condition of the umbilical arteries in the Indian domestic goat when five kids (two females and three males) were being dissected at an examination in Allahabad. In all of these five kids the umbilical arteries, each invested in a fold of the peritoneum and loosely attached to the wall of the urinary bladder, were as shown in the accompanying figure (kindly drawn for me by Mr B. K. Das, M.Sc.). Each



umbilical artery is given off, as in the sheep, from the base of the internal iliac, from which point of origin the uterine artery also arises. In the sheep and many other Mammals the umbilical artery is merely represented by its branches to the bladder, the original main trunk at most persisting (in the horse[1] and cat[2], e.g.) as a "fibrous cord" extending to the fundus of the bladder

[1] See *The Comparative Anatomy of the Domesticated Animals*, by A. Chauveau, 1891.

[2] St George Mivart, *The Cat*, 1881; also the *Anatomy of the Cat*, by J. Reighard and H. S. Jennings, 1901.

and navel, but in the common Indian goat each umbilical artery maintains a uniform diameter (nearly twice the size of the artery labelled internal iliac) for about 5 cms. and then suddenly ends blindly in the manner shown. From three to five vesicular arteries are given off towards the end of each umbilical artery. This same condition of the umbilical arteries was also found to exist in two other kids (sex unrecorded) and in adult goats (two specimens examined, both males). I injected several of these umbilical arteries with carmine fluid to determine if any outlet existed at the extremities but all results were negative.

The number of individuals, without exception, in which these peculiar umbilical arteries were found precludes the idea that they are individual abnormalities, and this fact may prove of some use in practice, since these umbilical arteries, occurring in such a common animal, would, as Professor Bayliss suggested to me, be extremely serviceable in connection with blood pressure experiments. I have not been able to discover any other instances in Vertebrates of arteries ending blindly in this fashion.

FISSURAL PATTERN IN FOUR ASIATIC BRAINS

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THE specimens here delineated are from the racial series in the Museum of the Royal College of Surgeons of England, and for the privilege of examining them I am indebted to the kindness of Professor Keith.

They consist of a Chinese brain, a Japanese, a Goanese, and an Arabian.

The drawings have been prepared in exactly the same way as those of three Chinese brains given in my paper in this *Journal* in 1911 (vol. XLVI, p. 54). That is to say, the pictures of the mesial and basal surfaces are tracings from photographs, modified only so far as to indicate, by a slight break in the line of a sulcus, the presence and position of any bridging gyrus concealed within it. The picture of the convex surface, on the other hand, besides giving such indications of deep gyri, departs so much in another respect from photographic outline that it has become "a sort of Mercator's projection" after Kohlbrugge's manner[1]. From a photograph of the lateral aspect of the hemisphere, taken perpendicularly to a sagittal plane, a tracing has been made, which has then by freehand drawing been extended upwards and at both ends so that the resulting picture, besides showing all that appeared in full view in the preliminary photograph, gives an equally full view of the vertex of the hemisphere and of the frontal and occipital poles. The upper border of the drawing accordingly represents, not the crest of the hemisphere as seen from the side, but the flat part of the mesial surface as seen edgeways from above. In the process of extending the drawing, the circumferential pole-to-pole dimensions of the parts all along the crest of the hemisphere have been unavoidably exaggerated; but their transverse dimensions, radial in the drawing, have been kept to the original scale. Except by some such device as this, a comprehensive record of the fissural pattern could not be given without cumbersome and costly multiplication of pictures from numerous points of view.

The Arabic figures upon the drawings give the approximate depth of the sulci in millimetres at the points against which they are placed. The Roman figures are marks by which we may identify corresponding points in two views of the same hemisphere.

I give no formal description of the specimens, but notes on some points which the pictures themselves do not reveal. No weights are given; they would be valueless, if only because the strength of the hardening fluids employed is not known, nor how long the specimens had remained first in formalin and then in spirit. The maximum sagittal diameter of the hardened hemisphere, taken in conjunction with the pictures of the mesial and basal surfaces, permits, however, a rough estimate of size. The other customary

[1] J. H. F. Kohlbrugge, *Die Gehirnfurchen Malayischer Völker*, Amsterdam, 1909, p. 11.

measurements are dispensed with, partly because of some distortion of the specimens, but also on general grounds, notably the want of fixed points, from which alone such measurements, if they are to have value, can be taken.

Chinese Brain D (figs. 1–5). Yu Ling, male, aet. 29, South China.

Left Hemisphere.—Maximum sagittal diameter, 163 mm.

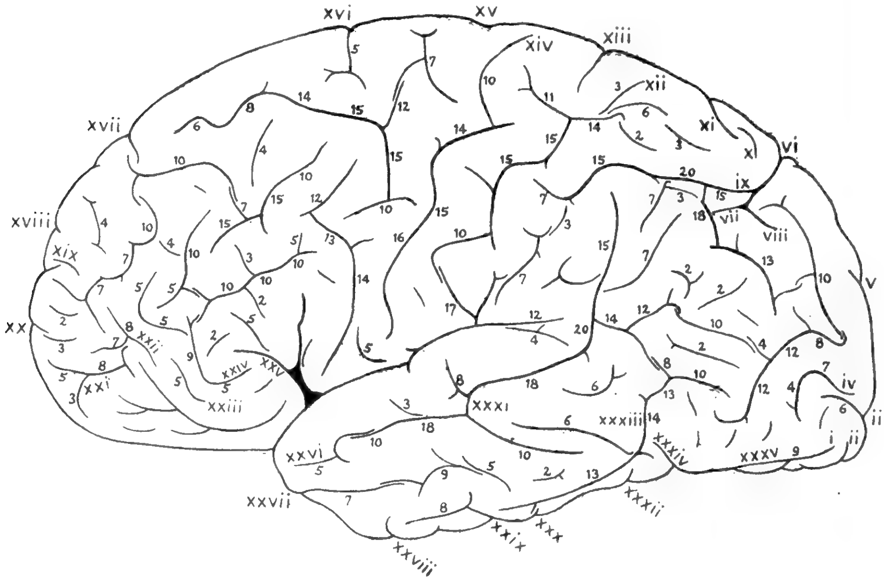

Fig. 1. D.

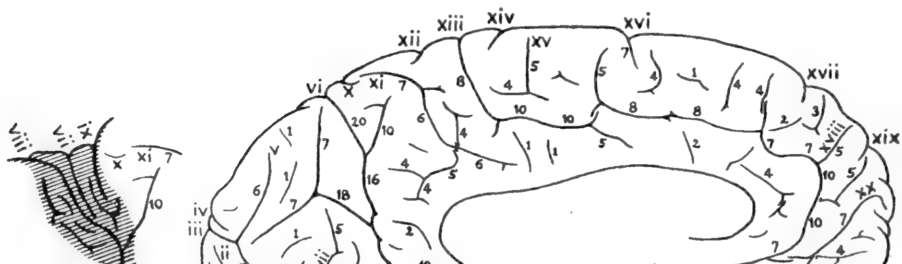

Fig. 2. D.

In the border of the orbital operculum there is one considerable notch, having the shape of an obtuse angle.

A little behind the lower end of the sulcus centralis, the border of the fronto-parietal operculum shows a notch, the end of a furrow that runs out from the superior limiting sulcus of the insula.

The incisura parieto-occipitalis (vii) extends outwards to join the intraparietal sulcus, but the depth to which it cuts the superior surface of the arcus parieto-occipitalis is only about 4 mm.

The intraparietal sulcus shows the oft-described appearance of three arches, but, as will be seen from the drawing, the middle arch is specious merely.

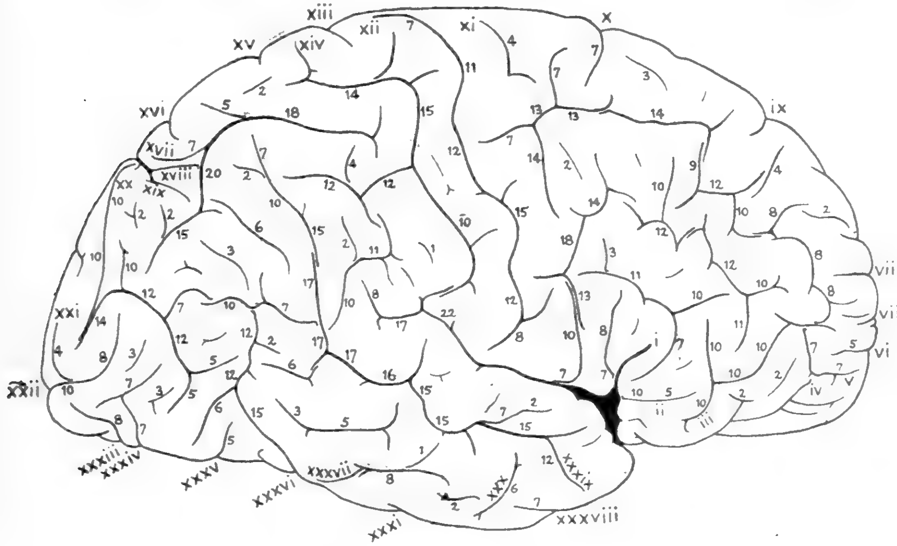

Fig. 3. D.

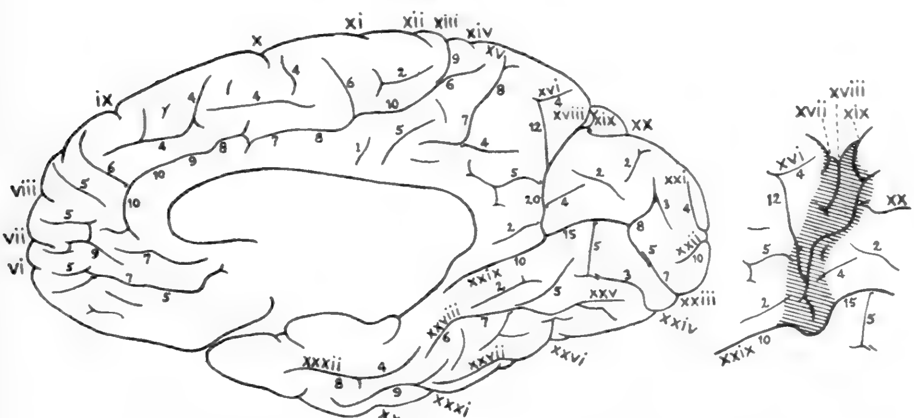

Fig. 4. D.

There are pronounced interdigitations in the superior and inferior frontal sulci; in the sulcus centralis, throughout its length; in the sulcus temporalis superior, especially near the origin of a posterior branch 14 mm. deep; and in the sulcus lunatus. Interdigitations are well marked in all that part of the sulcus cinguli anterior to Eberstaller's Brücke 3, especially at the place where

Brücke 2 would be looked for; at this place the interdigitations are associated with the appearance of notches in the lips of the sulcus; these notches are indicated in fig. 2.

The gyrus cunei is well developed.

Right Hemisphere.—Maximum sagittal diameter, 163 mm.

In the border of the orbital operculum, about opposite the middle of the sulcus orbitalis transversus of Weisbach, there is a pair of small notches.

Far back on the border of the fronto-parietal operculum, and indicated in the drawing just below a depth-mark 22, is a notch, the end of a sulcus that runs out from the superior limiting sulcus of the insula.

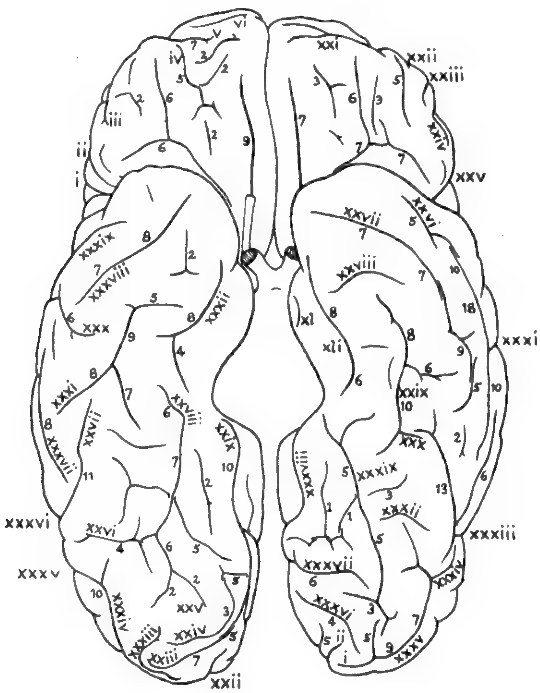

Fig. 5 D.

The incisura parieto-occipitalis (xviii) runs out to join the intraparieta sulcus, and cuts the superior surface of the arcus parieto-occipitalis to a depth nowhere less than 14 mm. There is a well-defined arcus intercuneatus turning beneath the inner end of the incisura (see inset to fig. 4).

The posterior end of the sulcus occipitalis paramesialis (xx) has a rather deep confluence with the upper end of the sulcus lunatus. The posterior lip of the sulcus lunatus overhangs the anterior lip in opercular fashion.

Interdigitations are well marked throughout the intraparietal, postcentral, superior temporal and superior frontal sulci; less well marked all along the sulcus centralis.

The gyrus cunei is well developed.

Japanese Brain (figs. 6–10). Male.

Left Hemisphere.—Maximum sagittal diameter, 151 mm.

The Sylvian fissure has a small anterior horizontal limb; and nearly oppo-

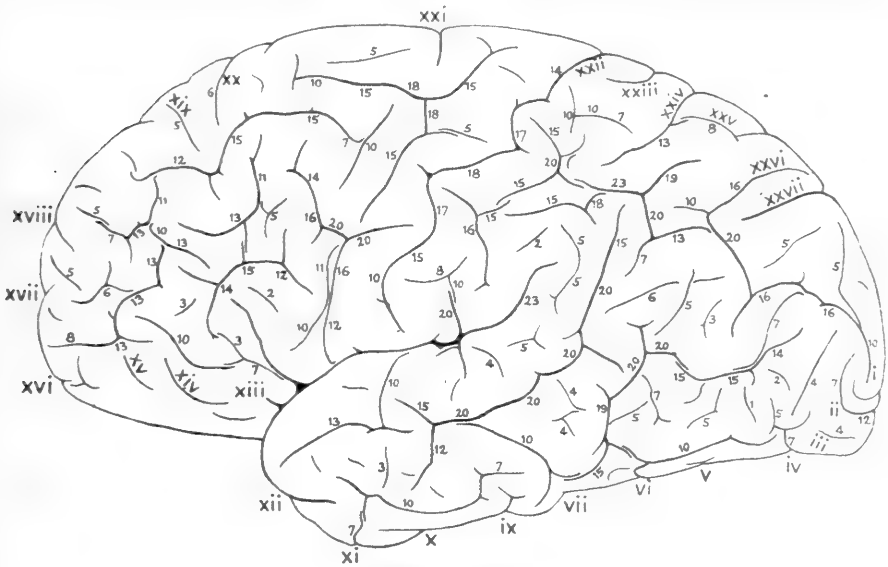

Fig. 6. Jap.

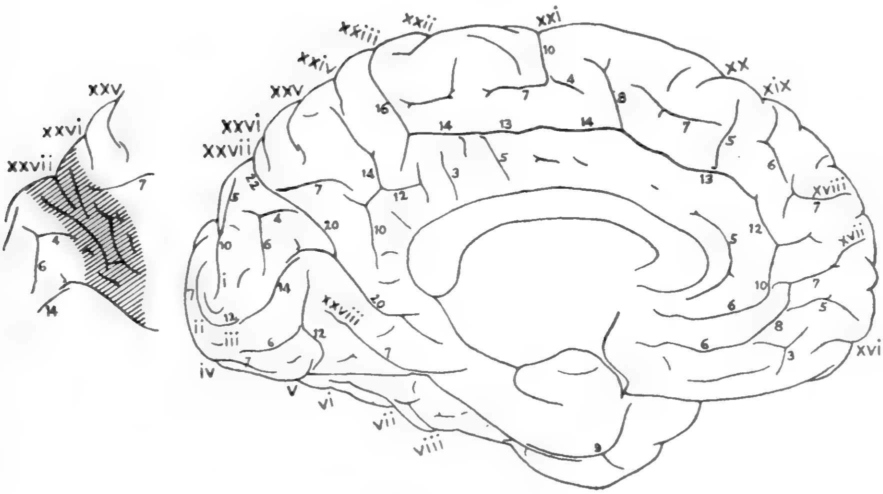

Fig. 7. Jap.

site the middle of the sulcus orbitalis transversus the border of the orbital operculum has a small notch (indicated in fig. 10).

Behind the lower end of the sulcus centralis, the border of the fronto-parietal operculum shows a small notch, the end of a furrow that runs straight

out from the superior limiting sulcus of the insula. The sulcus 20 mm. deep, immediately behind this notch, fails to reach the superior limiting sulcus.

Heschl's transverse gyri are well developed.

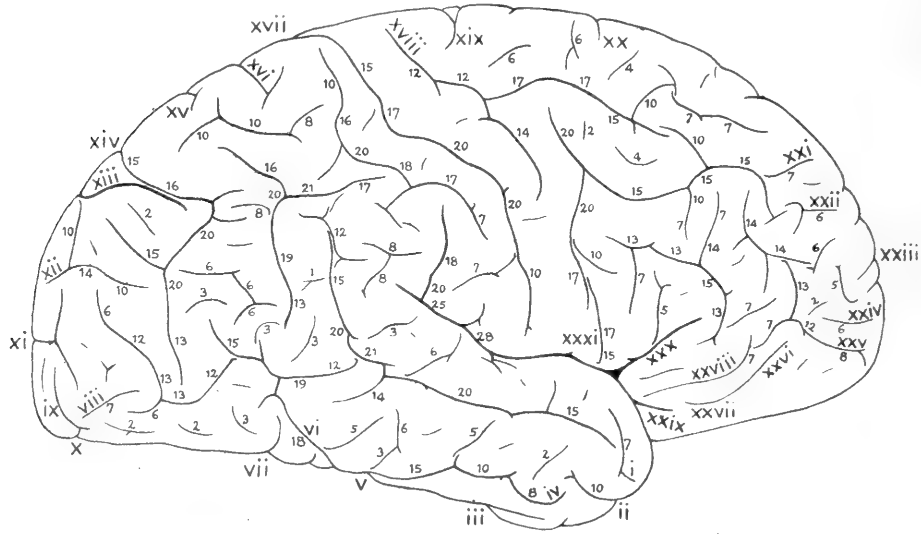

Fig. 8. Jap.

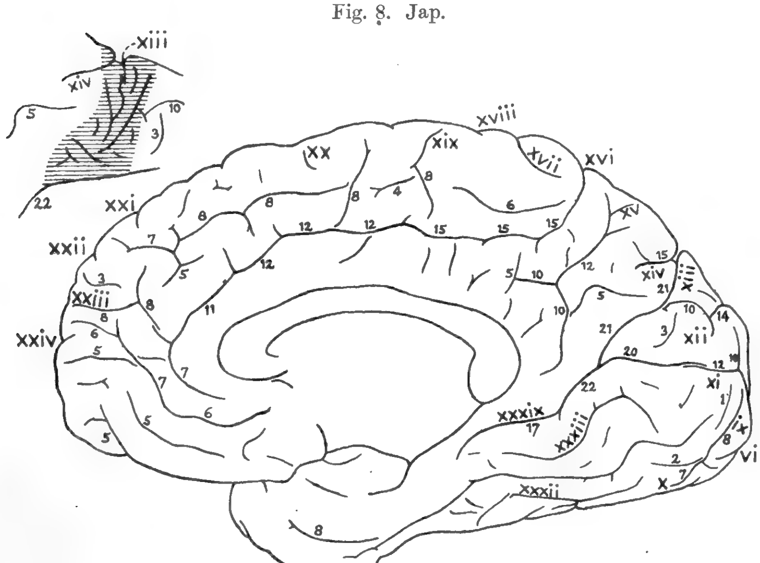

Fig. 9. Jap.

All the deep gyri indicated in fig. 6 in the intraparietal and postcentral sulci are very well defined. Interdigitations are strongly marked in the intraparietal, superior postcentral, superior precentral and superior frontal sulci, and throughout the sulcus centralis. There is an absence of deep bridging gyri in the sulcus cinguli, but there are many slight interdigitations.

On the inner aspect of the occipital pole is a well defined impression of the superior longitudinal venous sinus. The upturned end of the calcarine sulcus lies in this impression, and so comes to appear in fig. 6, but it does not invade the convexity proper.

The gyrus cunei is well developed.

The rhinal fissure has shallow confluence with the incisura temporalis and with the collateral sulcus.

Right Hemisphere.—Maximum sagittal diameter, 148 mm.

There are no notches in the border of the orbital operculum.

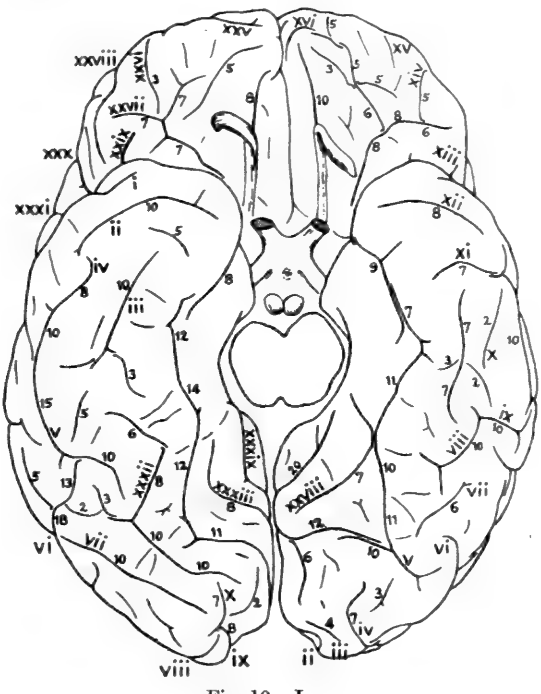

Fig. 10. Jap.

In the border of the fronto-parietal operculum are seen two notches, the terminations of two furrows that run out from the superior limiting sulcus. One appears near "xxxi," and the other just behind "28."

Heschl's transverse gyri are well developed.

Interdigitations are fairly well marked in the middle third of the sulcus centralis, and throughout the sulcus frontalis superior. They are well developed throughout the precentral, postcentral and superior temporal sulci. There is an absence of deep gyri in the sulcus cinguli.

In the parieto-occipital fossa there is no definite arcus intercuneatus.

The gyrus cunei is fairly well developed.

In each hemisphere the sulcus rhinencephali inferior of Retzius is faintly marked.

Brain of a Native of Goa, India (figs. 11–15). Male. Age unknown, "but not old."

Left Hemisphere.—Maximum sagittal diameter, 169 mm.

In the border of the orbital operculum there is one considerable notch, situated in a sagittal plane about 5 mm. internal to the outer extremity of the sulcus orbitalis transversus.

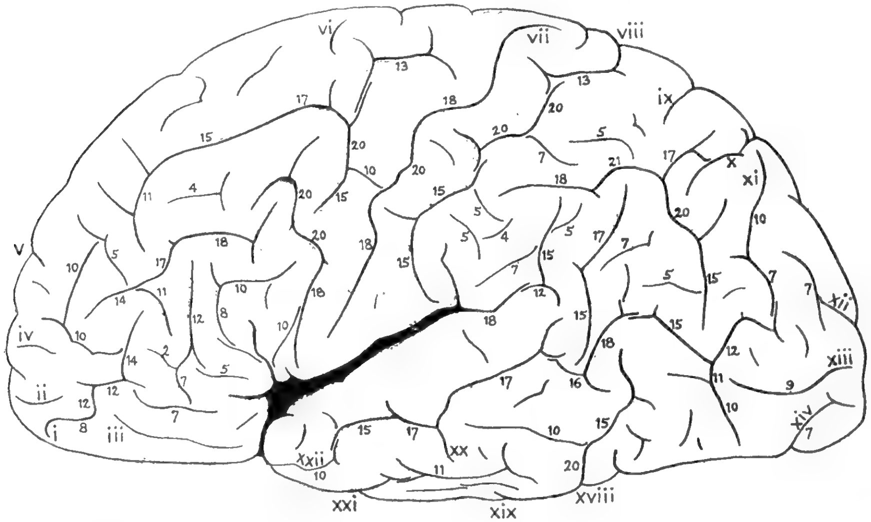

Fig. 11. Goa.

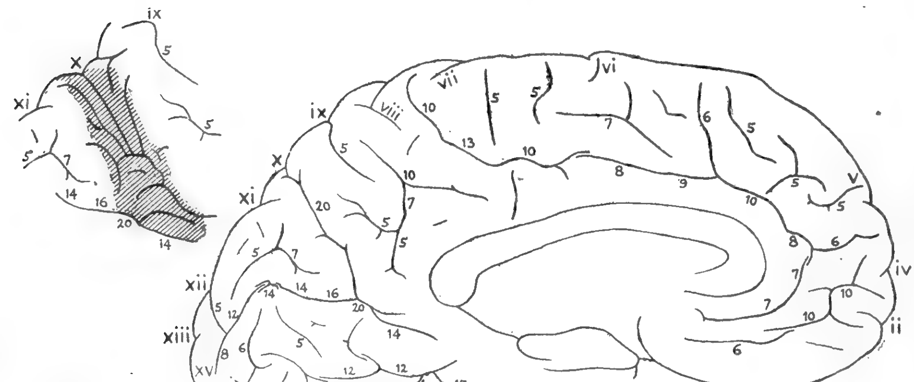

Fig. 12. Goa.

The upper end of the sulcus diagonalis has a superficial connection with the inferior precentral sulcus, and its lower end runs into the anterior ascending Sylvian limb.

In the internal arrangements of the parieto-occipital fossa there is some suggestion of an arcus intercuneatus and its accompanying sulci. In fig. 11 a

notch is shown which establishes a superficial connection between the parieto-occipital fissure and an ascending branch of the intraparietal sulcus lying close in front of it. This branch is partly shown also in the inset to fig. 12,

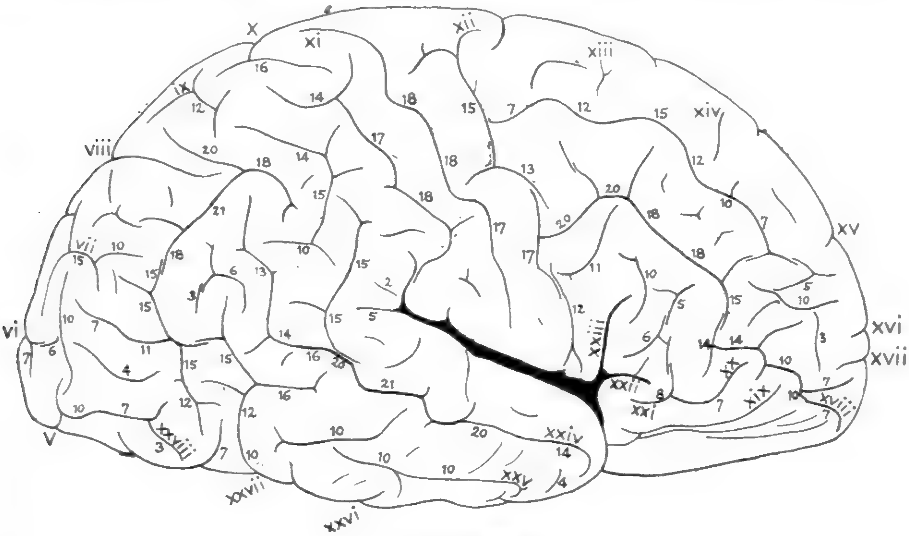

Fig. 13. Goa.

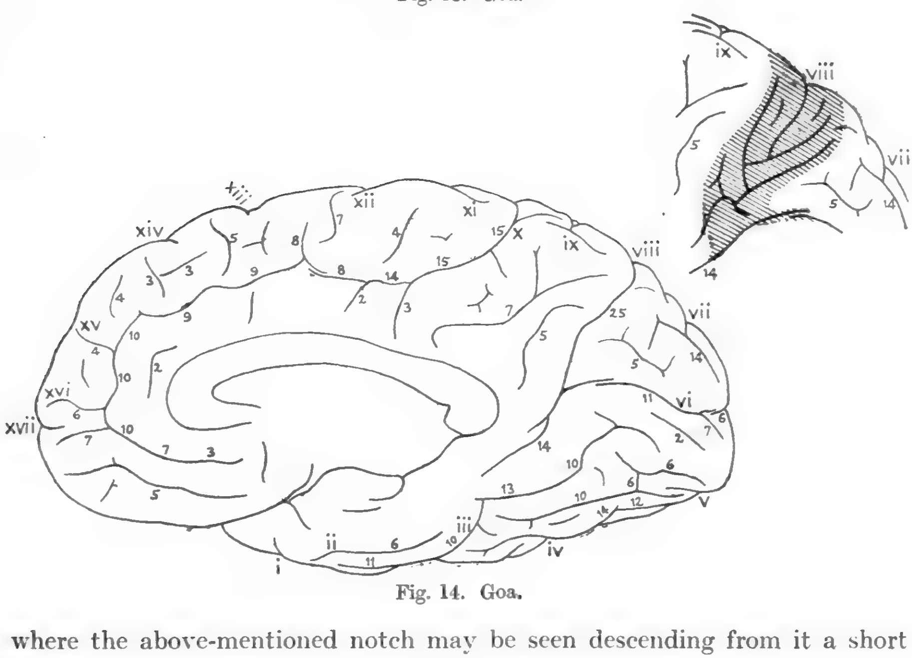

Fig. 14. Goa.

where the above-mentioned notch may be seen descending from it a short distance into the parieto-occipital fossa (shaded area).

The gyrus cunei is very well developed.

Interdigitations are strongly marked in the intraparietal, postcentral and

inferior precentral sulci; well marked in the sulcus temporalis superior and all along the sulcus centralis; less well marked in the sulcus frontalis superior.

The rhinal fissure is well developed, and joins the incisura temporalis (fig. 12).

Right Hemisphere.—Maximum sagittal diameter, 166 mm.

In the border of the orbital operculum there are two slight notches, one in a sagittal plane with each of the two anterior branches of the sulcus orbitalis transversus. The inner one of these notches appears in fig. 15.

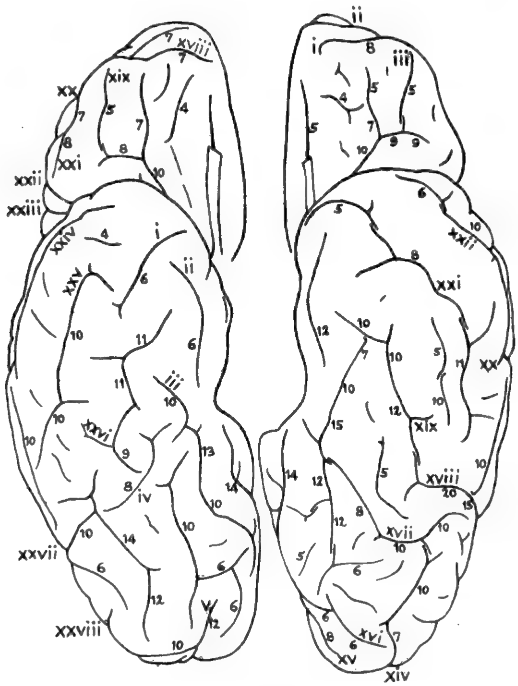

Fig. 15. Goa.

Rather far back on the border of the fronto-parietal operculum is a notch, the termination of a furrow that runs out from the superior limiting sulcus.

Interdigitations are well marked in the intraparietal, postcentral and superior temporal sulci, in the sulcus centralis, and in that part of the sulcus cinguli that lies anterior to Brücke 2. They are not very well marked in the sulcus frontalis superior.

The gyrus cunei is very well developed.

Brain of a Native of Arabia (figs. 16–20). Hamid Naggi, male, aet. 30. "Dark, and probably half negro." Died in England, of tuberculosis and peritonitis.

Presumably to facilitate penetration by the hardening fluid, the mesial surface of each hemisphere has been incised and the gash stuffed with wool,

crushing the corpus callosum and adjacent parts. In figs. 17 and 19, the gaping chasms are shown in solid black, across which some broken white lines have been drawn to connect portions of sulci properly continuous.

Left Hemisphere.—Maximum sagittal diameter, 166 mm.

Besides the large anterior ascending limb of the Sylvian fissure there is a small anterior horizontal limb (figs. 16 and 20). There are no notches in the border of the orbital operculum.

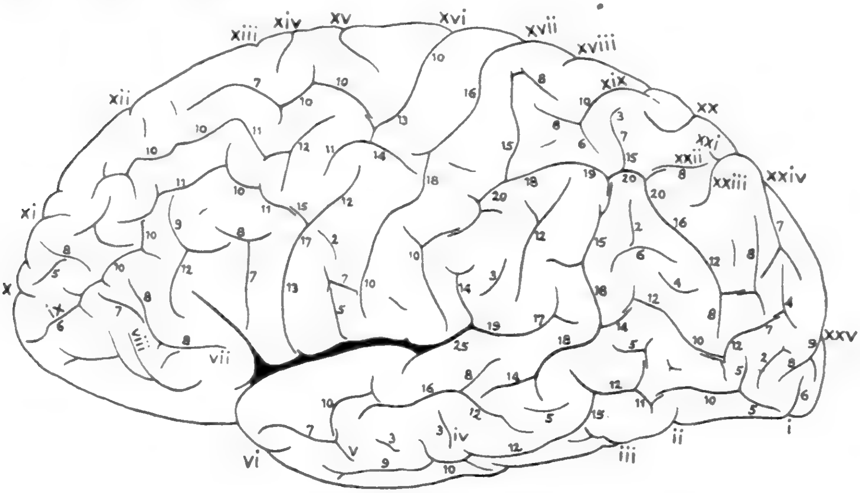

Fig. 16. Hamid Naggi.

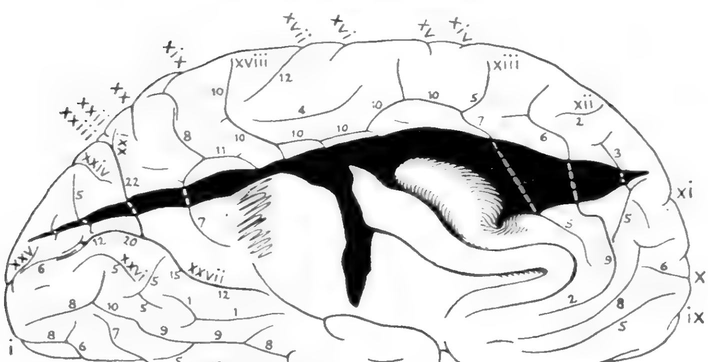

Fig. 17. Hamid Naggi.

In the border of the fronto-parietal operculum, a little behind the lower end of the sulcus centralis, there is a notch, the termination of a furrow that runs out from the superior limiting sulcus.

Interdigitations are present throughout the sulcus centralis. They are well marked in the superior and middle frontal sulci, the postcentral and intraparietal sulci, and the superior and middle temporal sulci.

The gyrus cunei is well developed.

The sulcus rhinencephali inferior is fairly well defined.

Right Hemisphere.—Maximum sagittal diameter, 163 mm.

The outer root of the sulcus olfactorius has a superficial connection with a sulcus which runs outwards and forwards towards the middle of the sulcus orbitalis transversus.

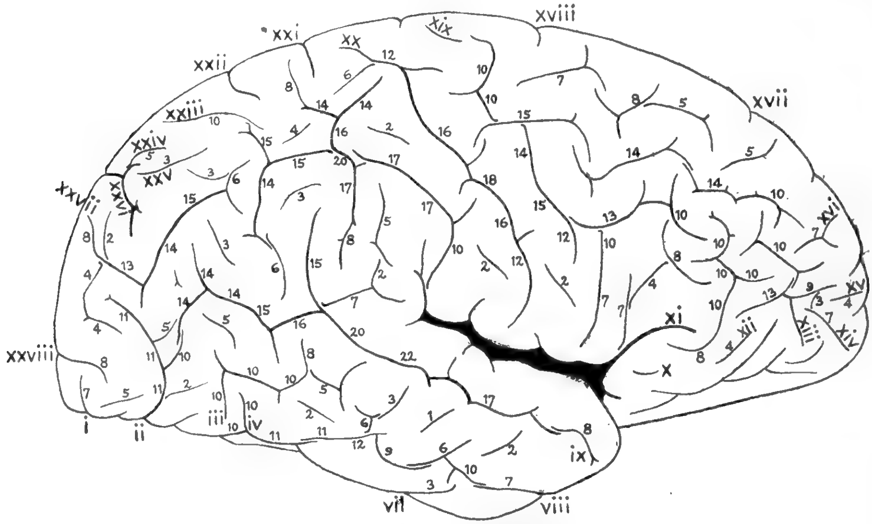

Fig. 18. Hamid Naggi.

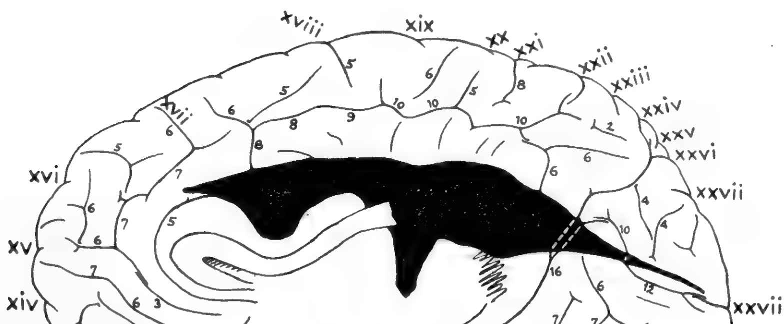

Fig. 19. Hamid Naggi.

There is a large anterior ascending limb of the Sylvian fissure (xi). And there is an orbital limb, which in the basal view (fig. 20) is seen emerging from beneath the temporal pole, behind that point in the sulcus orbitalis transversus against which a depth-mark 8 is placed.

The border of the fronto-parietal operculum is notched by two small sulci, one a little behind and the other a little in front of the lower end of the sulcus centralis. The posterior of these runs out from the superior limiting sulcus

The anterior, just within the Sylvian fissure, has a shallow connection with a sulcus that joins the superior limiting sulcus.

Interdigitations are well marked in the superior frontal and superior temporal sulci. They are present throughout the sulcus centralis. They are less pronounced in the intraparietal sulcus.

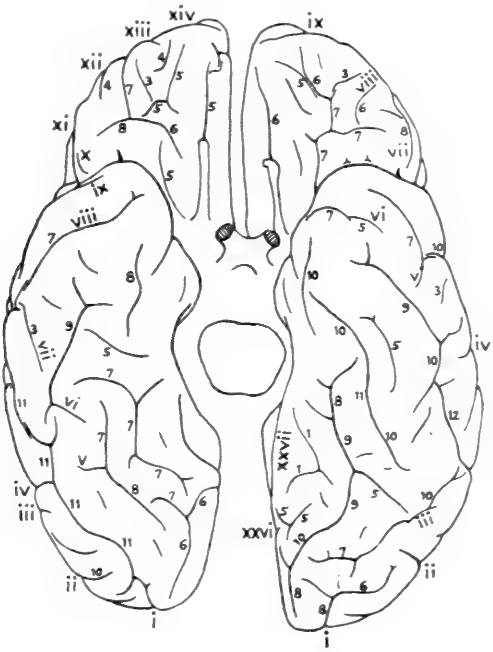

Fig. 20. Hamid Naggi.

The posterior lip of the sulcus lunatus overhangs the anterior lip considerably, in opercular fashion. On raising it, a bold buttress is seen on the anterior wall of the sulcus, immediately above the origin of an anterior branch 10 mm. deep.

The gyrus cunei is well developed.

The sulcus rhinencephali inferior is faintly marked.

FURTHER OBSERVATIONS ON THE GASTRO-INTESTINAL TRACT OF THE HINDUS

By Dr N. PAN,

Professor of Anatomy, Medical College, Calcutta, India

In my last paper published in the *Journal of Anatomy* (vol. LIII. Parts 2 and 3, April, 1919), I embodied the results of my observations on 65 cases. Subsequently, I continued my observations in the same line on additional 84 cases and the conclusions derived from the first series of 65 cases have been mostly corroborated.

The subjects in the present series are also Hindus, living on bulky Carbohydrate food. The method of preservation has been the same, viz., a preliminary injection of 8 oz. of Formalin after death followed after 24 hours by an injection of a solution of Arsenic.

STOMACH

Capacity of the Stomach. In Table A, the stomachs of both males and females have been arranged in order of increasing capacity. It shows that the capacity is very variable, ranging from 6 oz. to 200 oz., giving an average of 75 oz. In 54 out of these 84 cases (i.e. in 64 per cent.) the capacity is over 50 oz. Taking the two series of cases together ($65 + 84 = 149$ cases) the average capacity comes to 73·5 oz. Thus in Hindus, the average capacity of the stomach is much bigger than in Europeans and may be definitely said to lie between 70 and 80 oz.

In Table B, female stomachs have been arranged in order of increasing capacity. In this series, there are 23 subjects and the capacity ranges from 8 to 154 oz., giving an average of 59 oz. In my first series of 29 female subjects, the average capacity was 60 oz. Taking the two series together the average comes to 59·7 oz.

In Table C, stomachs of male subjects have been arranged in order of increasing capacity. The capacity ranges from 6 to 200 oz., giving an average of 81 oz. In my first series of 36 male subjects the average capacity was $80\frac{1}{2}$ oz. So the results of the two series tally with each other very closely. Now, it may be definitely stated that the capacity of male stomachs is much bigger than that of the female stomachs. In females, the average capacity is 60 oz., whereas, in males it is roughly 80 oz. This difference in the capacity of the stomachs in the two sexes may be explained by observing the social custom of the Hindus. The members of a family take their food in batches; the male members take their meals first, and the female members in the last batch,

Table A.

Stomachs of both sexes arranged in order of increasing capacity.

No.	Sex	Length in inches	Greatest width in inches	Capacity in ounces	No.	Sex	Length in inches	Greatest width in inches	Capacity in ounces
1	M.	7	3	6	43	M.	12	6	80
2	M.	7½	4½	7½	44	M.	11½	5	80
3	F.	7½	4	8	45	M.	11	6	80
4	F.	7	4	9	46	F.	11	6	80
5	F.	7	2½	10	47	M.	12½	5	80
6	M.	5½	4	12	48	M.	11	7	82
7	F.	8	4	12	49	M.	11	7	85
8	F.	8	5	14	50	M.	12	6	88
9	M.	8	4	15	51	M.	12	8	93
10	M.	7	3½	16	52	F.	12	7	96
11	F.	9½	4	21	53	M.	11	7	96
12	M.	7½	4½	22	54	F.	11	6	96
13	F.	10	4½	22	55	M.	11½	6	96
14	M.	6	4	24	56	F.	12	7	96
15	M.	7¼	4¼	25	57	M.	15	5	98
16	M.	10	4½	30	58	M.	12	5	102
17	F.	8	5	32	59	M.	11	7	104
18	M.	10	6	32	60	M.	12½	6½	104
19	F.	9½	5	33	61	M.	13	6½	104
20	M.	10	5	40	62	M.	12¼	6	104
21	M.	8½	5	40	63	M.	13	8	104
22	F.	11	7	40	64	M.	12	8	105
23	F.	8	4½	41	65	M.	13	6	105
24	M.	10	4¾	43	66	F.	12	8	105
25	M.	9½	5	43	67	M.	13	6	106
26	M.	9	5	45	68	M.	14	8	106
27	M.	8½	4½	46	69	M.	14	6	109
28	M.	10	7	48	70	M.	13	8	110
29	F.	9	5	48	71	M.	14	8	110
30	M.	11	8	48	72	M.	15	8	112
31	M	12	5	58	73	F.	16	9	119
32	F.	9	5	58	74	M.	12	9	120
33	F.	8	6	60	75	M.	14	5½	130
34	M.	12	5	60	76	M.	14½	6½	132
35	M.	9	5	62	77	F.	14½	5½	132
36	M.	12	3½	62	78	M.	12½	8	135
37	M.	10	5½	68	79	M.	15	11	139
38	F.	10	6	70	80	M.	17	6	144
39	M.	11½	7	70	81	F.	15½	8½	154
40	M.	12	6½	70	82	M.	14	8	180
41	M.	10½	6	72	83	M.	15	9	180
42	M.	12	7	80	84	M.	20	7	200

Table B.

Female stomachs arranged in order of increasing capacity.

No.	Length in inches	Greatest width in inches	Capacity in ounces	No.	Length in inches	Greatest width in inches	Capacity in ounces
1	7½	4	8	13	9	5	58
2	7	4	9	14	8	6	60
3	7	2½	10	15	10	6	70
4	8	4	12	16	11	6	80
5	8	5	14	17	11	6	96
6	9½	4	21	18	12	7	96
7	10	4½	22	19	12	7	96
8	8	5	32	20	12	8	105
9	9½	5	33	21	16	9	119
10	11	7	40	22	14½	5½	132
11	8	4½	41	23	15½	8½	154
12	9	5	48				

Table C.

Male stomachs arranged in order of increasing capacity.

No.	Length in inches	Greatest width in inches	Capacity in ounces	No.	Length in inches	Greatest width in inches	Capacity in ounces
1	7	3	6	32	11	7	82
2	7½	4½	7½	33	11	7	85
3	5½	4	12	34	12	6	88
4	8	4	15	35	12	8	93
5	7	3½	16	36	11	7	96
6	7½	4½	22	37	11½	6	96
7	6	4	24	38	15	5	98
8	7¼	4¼	25	39	12	5	102
9	10	4½	30	40	11	7	104
10	10	6	32	41	12½	6½	104
11	10	5	40	42	13	6½	104
12	8½	5	40	43	12¾	6	104
13	10	4¾	43	44	13	8	104
14	9½	5	43	45	12	8	105
15	9	5	45	46	13	6	105
16	8½	4½	46	47	13	6	106
17	10	7	48	48	14	8	106
18	11	8	48	49	14	6	109
19	12	5	58	50	13	8	110
20	12	5	60	51	14	8	110
21	9	5	62	52	15	8	112
22	12	3½	62	53	12	9	120
23	10	5½	68	54	14	5½	130
24	11½	7	70	55	14½	6½	132
25	12	6½	70	56	12½	8	135
26	10½	6	72	57	15	11	139
27	12	7	80	58	17	6	144
28	12	6	80	59	14	8	180
29	11½	5	80	60	15	9	181
30	11	6	80	61	20	7	200
31	12½	5	80				

partake of the remains of a meal which are usually insufficient. Thus they are often underfed, resulting in a reduction in size of their stomachs.

My observations on the stomachs of stillborn full term foetuses are yet incomplete.

Measurements of Stomachs

Table A shows the measurements in both males and females. The length varies considerably giving an average of 11·1 inches in both sexes taken together. In my first series of 65 cases, the average length was 11·25 inches. So, here also the result of my previous observation has been corroborated. As regards the breadth, the average of this series comes to 6 inches, and this corroborates my previous statement that the increase in the breadth of the stomach of the Hindus is more marked than the increase in length.

DUODENUM

Observations have been made on the same 84 subjects (Tables D and E). In both males and females taken together, the average length of the Duodenum is found to be 9·4 inches. This also tallies with the result of my previous observation, showing that the average length of the Duodenum in Hindus is less.

JEJUNUM AND ILEUM

The average length of the Jejunum and Ileum in both males and females taken together (Tables D and E) is found to be 20 ft 7 inches. Adding to this 9·4 inches, the average length of the Duodenum, the average length of the Small Intestine is found to be 21 ft 4½ inches. This approaches closely the result of my observation on the first series of 65 cases, in which the average length came to 21 ft 9½ inches. Thus it confirms my statement that the average length of the Small Intestine of the Hindus is less than in Europeans. Taking the average length of the Small Intestine of females only (Table D), the average is found to be 19 ft 9½ inches. Here the results of the two series of female cases have been conflicting. For, in my first series of 29 female cases, the average length was found to be 22 ft 1½ inches. So no definite statement can be made regarding the length of the Small Intestine in females here, until further observations are carried out on a larger number of cases.

Aggregated Lymph Nodules (Peyer's Patches)

Taking the male and female subjects together (Tables D and E), the average number is found to be 21. Thus it confirms my statement that the average number here lies between 20 and 30.

Vermiform Process

The length of the Vermiform Process has been noted in the same 84 subjects (Tables D and E). The average length in these cases is nearly 3 inches. Taking the average of 149 cases (first and second series together) the length

Table D.

Female subjects.

No.	Length of Duodenum in inches	Length of Jej. and Ileum in feet	Length of V. Appendix in inches	Number of Peyer's Patches	Length of L. Intestine in feet	Mesocoecum	Mesocolon Ascending	Mesocolon Descending
1	8	14½	3	24	4¼	nil	nil	pres.
2	7	13½	2½	15	2⅓	nil	nil	nil
3	7	14⅓	2	23	4½	nil	nil	pres.
4	10	19¼	2½	13	2½	pres.	nil	nil
5	8	20¾	2	8	4½	nil	nil	pres.
6	8	8½	2	11	3	nil	nil	nil
7	10	22	2½	15	5½	nil	nil	nil
8	10	20	2½	20	7	nil	nil	nil
9	10	25½	2½	33	4½	nil	nil	nil
10	8	18	2	17	3	nil	nil	pres.
11	8	20½	1	57	6⅓	nil	nil	nil
12	10½	23	2½	20	6	nil	nil	nil
13	10	13½	2½	20	3½	nil	nil	pres.
14	12	20	1½	23	3½	pres.	pres.	pres.
15	9	20¾	2¼	27	6¼	nil	pres.	pres.
16	11½	12	2	8	4	pres.	pres.	pres.
17	11	21¼	4½	28	7⅓	nil	nil	nil
18	7½	17	2	21	4	nil	nil	nil
19	10	20	4½	23	6½	nil	nil	nil
20	11	16¼	5	14	5¼	nil	nil	nil
21	12	21	4	13	6	pres.	pres.	pres.
22	9½	22	5	15	5	nil	nil	nil
23	9½	25	1½	13	4¾	nil	pres.	pres.

Table E.

Male subjects.

No.	Length of Duodenum in inches	Length of J•j. and Ileum in feet	Length of V. Appendix in inches	Number of Peyer's Patches	Length of L. Intestine in feet	Mesocoecum	Mesocolon Ascending	Mesocolon Descending
1	10½	22	4	24	6	nil	nil	nil
2	7	19	2	26	4¼	nil	nil	nil
3	7	16¼	3½	19	4⅓	nil	nil	nil
4	7	24	2	23	4	nil	nil	nil
5	10	16½	2	5	3½	pres.	pres.	pres.
6	8	13⅓	2½	0	4½	nil	nil	pres.
7	5	24½	3	28	5¼	nil	nil	nil
8	11½	16¾	3	16	3¾	nil	nil	nil
9	10	18⅓	2	27	4½	nil	nil	nil
10	9½	12	3	12	3⅓	nil	nil	nil
11	9	21	2	25	4½	nil	nil	nil
12	11	21¾	3	8	5	nil	nil	nil
13	8	24	2	22	5	nil	nil	nil
14	12	23	2½	5	5¼	nil	nil	nil
15	10	16½	4	37	3	nil	nil	nil
16	9	22¼	4¾	12	4¼	nil	nil	nil
17	11	19½	3	17	7⅓	nil	nil	nil
18	8	16¾	3	19	3½	nil	pres.	pres.
19	10	21	4	25	4	nil	nil	nil
20	10	17½	2	25	5	nil	nil	nil
21	9½	18	3½	16	3¾	nil	nil	nil
22	9	21½	3	28	4	nil	nil	nil
23	7½	27¼	4	21	3¾	nil	pres.	nil
24	10	21¾	5	26	4	nil	nil	nil
25	9	15½	2¾	20	4	nil	nil	nil
26	9	27½	2¾	29	5½	nil	nil	nil
27	9½	20	3	10	7	nil	nil	nil
28	9	29	3	21	5¼	nil	nil	nil
29	10	22	2½	25	6	nil	nil	nil
30	6	18	2	27	3	nil	nil	nil
31	11	32	1½	21	5½	nil	nil	nil
32	11½	19	3	25	4¼	pres.	pres.	pres.
33	8	21⅓	4½	12	5¾	nil	nil	nil
34	9½	16	2½	29	4½	nil	nil	nil
35	8½	19½	2	38	4	pres.	pres.	nil
36	6	23¾	2	34	4¾	nil	nil	pres.
37	9	25½	4	32	4½	nil	nil	nil
38	9	25	2½	20	4½	nil	pres.	nil
39	9	17½	2¾	18	4¾	pres.	pres.	pres.
40	10	13¾	3¾	3	3½	nil	nil	nil
41	12	19	2	25	5	nil	nil	nil
42	11½	24	4	23	5⅓	nil	nil	nil
43	8½	21½	2½	32	4	nil	nil	nil
44	8	21	4	34	4½	nil	nil	nil
45	9	25	3¼	20	6½	nil	nil	pres.
46	11	22⅓	4½	27	4	nil	nil	nil
47	11	26	3½	29	5¾	nil	nil	pres.
48	11	24	4	34	4⅓	nil	nil	nil
49	8½	21¼	4	14	5	nil	pres.	pres.
50	12	27	2¾	21	7	nil	nil	nil
51	9	20½	2	21	6¼	nil	nil	nil
52	11½	25	1½	37	8	nil	nil	nil
53	10	17½	3	16	4½	pres.	pres.	pres.
54	9½	22	5	15	5	nil	nil	nil
55	10	22¼	3½	15	5	nil	nil	nil
56	11	28	4½	23	9	nil	nil	pres.
57	12	24½	3½	23	5	nil	nil	nil
58	9	25	3	27	4½	nil	nil	nil
59	8½	15	2	20	3½	pres.	nil	nil
60	11	21½	2	25	4½	pres.	pres.	pres.
61	9	27	4	28	9½	nil	nil	nil

of the Vermiform Process is found to be 2·8 inches. So it confirms my statement that the average length of the Vermiform Process is less in Hindus. The largest Appendix found has been 5 inches.

As regards the position of the Vermiform Process, it has been found to occupy all possible positions, viz. (1) upwards and lateralwards, (2) vertically upwards, (3) upwards and medialwards, (4) horizontally medialwards, (5) downwards and medialwards, (6) vertically downwards, (7) downwards and lateralwards, (8) horizontally lateralwards. In 63 per cent. of these cases, it has been found directed upwards. In one case, the Vermiform Process $2\frac{1}{2}$ inches in length, was directed upwards and medialwards and lodged in a deep peritoneal recess. This recess was an unusual one (not the Inferior Ileocoecal pouch), and was situated below the Ileum, one inch to the left of the Ileocoecal junction, with its opening directed downwards and to the right. One and a half inches of the terminal part of the appendix was inside the pouch, and could not be drawn out as it was adherent inside the pouch, due perhaps to previous inflammation.

COECUM

The position of the Coecum has been noted in these 84 cases. In 7 cases, it has been found in the right Lumbar region just above the crest of the Ilium. In 4 subjects, it has been found 2 inches above the medial margin of the Psoas Major, at the brim of the lesser Pelvis. In one case it was hanging into the Pelvis. In the remaining 72 cases, its position was normal in the right Iliac Fossa.

LARGE INTESTINE including Rectum and Anal Canal

The length of the Large Intestine has been noted in the same 84 cases (Tables D and E). The length varies from 2 ft 4 inches to 9 ft 6 inches, giving an average of 4 ft 10 inches. The extremes found by other observers are not below 3 ft nor above 7 ft. But here the minimum length found in a female subject is 2 ft 4 inches, and the maximum length found in a male subject is 9 ft 6 inches. The greatest width has been usually found in the Coecum and the average greatest width in these cases has been $2\frac{1}{2}$ inches.

MESOCOECUM (Tables D and E)

Mesocoecum has been found in 11 out of these 84 cases, i.e. in 13 per cent. of males and females taken together. This confirms the result of my observation on the first series of 65 cases, in which it was found in 14 per cent.

ASCENDING MESOCOLON (Tables D and E)

Ascending mesocolon has been found in 15 out of these 84 subjects, i.e. in 17·8 per cent. of both males and females taken together. This confirms the result of my observation on the first series of 65 cases, in which Ascending Mesocolon was found in 17 per cent.

DESCENDING MESOCOLON (Tables D and E)

Descending Mesocolon has been observed in 23 out of these 84 cases, i.e. in 27 per cent. of both sexes taken together. In my first series of 65 cases, Descending Mesocolon was found in 21·5 per cent. It will be observed that a Descending Mesocolon has been found in a large percentage (43 per cent.) of the female cases of the present series (Table D).

Taking the average of 149 cases (first and second series), a Descending Mesocolon is found in 24·5 per cent.

The following table shows the results of the observations on the two series of cases separately, and the average of the two series considered together.

Table F.

	Stomach			Length of Duodenum	Length of Jejunum and Ileum	No. of Peyer's Patches	Length of Vermiform Process	Mesocolon	Mesocolon	
	Capacity	Length	Breadth						Ascending	Descending
(*a*) Average of first series of 65 cases ...	71·5 oz.	11·25″	5·8″	9·5″	21′	23	2·5″	14	17	21·5
(*b*) Average of second series of 84 cases...	75 oz.	11·1″	6″	9·4″	20′ 6″	20·8	2·94″	13	17·8	27·3
(*c*) Average of both series taken together	73·5 oz.	11·2″	5·9″	9·4″	20′ 9″	21·6	2·8″	13·4	17·4	24·5

CONCLUSION

The average total length of the intestinal canal in Hindus is thus calculated to be 26 ft, and is thus much less than the length noted in persons who take a greater proportion of meat and a smaller proportion of carbohydrate food.

In persons living on bulky carbohydrate food the intestinal canal is expected to be longer in order to accommodate a bulky refuse. Thus in herbivorous animals the intestinal canal is comparatively longer, whereas in carnivorous animals the intestinal canal is shorter but more muscular.

The experiments of Babak (cited from Madinavetia, *Physiologia Palleologica de la Digestion*, Madrid, 1910) have shown that in animals of the same species even, taken quite young and growing, if some are fed exclusively upon vegetable food and others mostly on meat a similar adaptation in length occurs, viz. a greater length in the animals fed on vegetable diet.

In Japanese and Chinese, who also live mostly on a bulky carbohydrate food, a marked increase in the length of the intestinal canal has been noted. But here taking the average of 149 cases, there is rather a decrease in the length of the intestinal canal observed. Thus it occurred to me that greater accommodation for the excreta may be provided by an increase in the breadth rather than an increase in length. So I noted the breadth as well in the second series of 84 subjects. The average greatest breadth of the small intestine in these cases has been found to be 1½ inches and that of the large intestine

$2\frac{1}{2}$ inches. So it is probable that the intestinal contents are comparatively rapidly ejected as they excite peristalsis mechanically by their bulk and nature and as such these vegetarians as a rule seldom suffer from constipation and the intestines rarely remain loaded.

In carnivorous animals a shorter vermiform process is found than in herbivorous animals. Consistently with this a larger vermiform process is expected to be present in vegetarians. But here it is shorter and it may be that the nature of the diet plays no part in determining the length of the vermiform process.

I thank my assistants, specially Dr Nagendra Nath Chatterjee, Assistant Professor of Anatomy, for their kind co-operation in carrying out these observations.

REVIEW

Cunningham's *Manual of Practical Anatomy*, Vols. I, II and III.

Seventh edition. Henry Frowde and Hodder and Stoughton.

As an example of the high standard of excellence to which the art of book-production can attain, this new edition of Cunningham's *Practical Anatomy* is superb. The original two-volumed manual is now published in three volumes, owing, we are told, to the introduction of many new illustrations of dissections, sections, and radiographs, and to the amplification of the instructions for dissection. The Basle nomenclature is retained throughout, while at the commencement of the first volume is a glossary of the two terminologies.

The descriptive part of the work is very complete, and the instructions to the dissector are clear and practical. We realise the advantages of the metric system in weights and measurements, but surely the literal translation of 1½ inches into 38 mm. gives the student an impression of unjustifiable accuracy.

The movements of joints are described in some detail, but we observe a departure from the usually recognised classification of joints by terming the sacro-iliac joint a diarthrosis, and the intercentral and intersternal as synchondrodial rather than symphysial joints. The radiographs of bones, joints, and injected arteries are well produced. The illustrations, both coloured and uncoloured, are extremely fine; indeed, it is doubtful whether they are not too fine. Experience shows that students who rely on illustrations for visual memorization, learn their anatomy in two dimensions, and possess but a feeble appreciation of depth.

And this raises the question as to whether a practical dissecting manual, by undue elaboration, does not tend to defeat its own ends. The aim of a dissecting manual is, we take it, to show the student how to set about displaying the various structures of the body, and, when displayed, how to identify them. It should draw his attention to points of use and interest which he might otherwise overlook, but it should direct his observation and not observe for him. It should aim at giving the student a correct sense of proportion, laying adequate stress on features of importance, and avoiding undue emphasis on unimportant structures. In connection with this point, we note that the description of the gleno-humeral ligaments implies that they are equally important as the coraco-humeral and other ligaments of the shoulder-joint. Lastly, a practical anatomy book should have due regard for the relatively limited time set apart for anatomy in the modern curriculum, a curriculum which is becoming more and more crowded with courses of instruction in the side-branches of medical science. We are far from agreeing with those who advocate the elimination from anatomical teaching of all details which have not a direct and obvious application to medical and surgical matters, but we think it must be admitted that there is a limit to the assimilative powers of the medical student, and we believe that this limit is overstepped by the elaborate detail and the unnecessary complexity of these volumes of practical anatomy. We remark, by way of illustration, that no less than four superficial patellar bursae are described, a subcutaneous, a subfascial and a subtendinous prepatellar bursa, and a subcutaneous infrapatellar bursa. Again, the diagram of the brachial plexus as given on page 40 of vol. I is one which no average medical student has the time to master during his dissections. In short, it seems to us that these books err in containing too much descriptive detail which overtaxes the student's powers, and too plentiful and too excellent illustrations which tend to replace the student's own powers of observation altogether. We are reminded of a certain elaborate type of guide-book which requires so much study and concentration that the sightseer has not the time to contemplate sufficiently the features which the book purports to point out.

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